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INTERACTIONS BETWEEN NEIGHBOURING PLANTS.

- Part I: Application of Grime's model of plants' ecological strategies to Agroforest System Design
- Part II: The use of z-scores in a distance based spatiotemporal dynamic model of interactions between plant neighbours: A step towards optimisation modelling of planting patterns and species mixtures in Agroforestry
- Part III: On the possibility and possible mechanisms of inter-specific cooperation between competing, neighbouring plants.

Thesis submitted for the degree of
Doctor of Philosophy

in the
Systems Department
Technology Faculty
Open University

by
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ABSTRACT

This thesis addresses the issue of interactions between neighbouring plants by looking at theory and models used in the study of wild plants with a view to applying them in the design of agroforests. In Part I difficulties of designing mixed crop stands are considered. Grime's model of the ecological strategies pursued by wild plants is described and its potential usefulness pointed out. Experimental results are presented suggesting that stress-tolerant trees may interfere less with an understorey component than do competitive trees through the different patterns of spatial occupation manifested by their roots.

Part II describes a statistical method to determine how any measurable attribute of one plant depends on the proximity and/or other characters of neighbouring plants. The method overcomes the need for unfeasibly large numbers of treatments encountered by conventional field trial methods.

The method has the potential to offer a firm basis for the design of optimized plant production systems; and will also allow ecologists to detect and quantify interactions between wild plants in the field.

Part III, using concepts of Evolutionary Game Theory, examines the question of cooperation in plants: both between the green plant and its associated vesicular-arbuscular mycorrhizal (VAM) fungi; and between neighbouring green plants connected by common VAM fungal hyphae. Exploring the implications for plants of Axelrod and Hamilton's (1981) Game Theoretic approach to the evolution of cooperative behaviour, it examines a logical problem in the view that the relationship between a green plant and associated VAM fungus is mutually beneficial. That the association is of mutual benefit would be insufficient to explain its persistence, and the fact that it does persist tells us something about its structure.

It is shown that no logical paradox exists in postulating the simultaneous existence of competition for resources and of resource-sharing cooperation between a given pair of neighbouring green plants; and that at least a certain minimal type of cooperation may be deemed to exist between connected plant neighbours. Putting together findings from two fields - direct nutrient transfers and biotic specialisation - solves problems for both, and provides evidence for inter-plant cooperation. Possible evolutionary stages through which cooperation could have passed are discussed. Given this theory it can no longer safely be *assumed* that plants do not cooperate, and experimental results are presented suggesting that they may be able to.

Scientific and economic implications are indicated for all three areas covered. Fertile ground exists for further research and suggestions are made for directions and methods.

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Chapter 1. General Introduction

It seems clear that our future uses of land will need to be more productive, yet, at the same time, more sustainable (i.e. better in conserving land fertility and other exhaustible natural capital - people, fertilisers, energy, benign species, genes) than those presently obtaining. Many management techniques are available which are more productive *or* sustainable. The main reason for mushrooming interest in Agroforestry lies in the claims that well-designed agroforests can combine productivity with sustainability.

Why are such claims made? I will take first the question of productivity. Due to the great difficulty of acquiring data on Agroforestry, the expectation of high yields is really mainly based on work with intercropping. Here, reported LERs (Land Equivalent Ratios¹) are far more frequently above, than below, unity (Willey, 1979). This is most generally understood in terms of *complementarity* of resource use: the more the patterns of resource capture (niches) of two neighbouring plants are dissimilar in time or space or composition, then the greater can be the captured fraction of total resources potentially available to them from their habitat. In the most usual case, intercropped land carries higher LAIs (Leaf Area Indices) for longer periods than does sole-cropped land. Since a mixture of trees with annuals appears more dissimilar than a mixture of annuals only, particularly in that the leaves and roots of trees do not have to climb a logistic curve from the beginning of the growing season, it may be that agroforests have larger LERs even than intercrops.

Reasons for expectations of sustainability from agroforests arose mainly from observations of very low rates of soil erosion occurring under forest cover. These have been ascribed to interception of rain-drops by trees and litter, and to the effects of root systems increasing the hydraulic conductivity of soils (and, therefore, their ability to reduce surface run-off), and increasing their retention of water (field capacity).

Another aspect of sustainability concerns fuel-wood production. Parts of Africa and Asia particularly have a serious and worsening problem of fuel-wood availability for rural dwellers. Attempts by governments to plant and protect trees have been highly unsuccessful because the peasantry have not been involved in the projects: it is not usually possible for central government to stop them using saplings for fuel or clearing forested land for farms. Later attempts to involve peasants through Community Forestry programmes usually foundered on class divisions: peasants find it hard to believe power-holders' assurances that they will be the beneficiaries of their work; and establishing trees

¹ The Land Equivalent Ratio is the unit area of land which would be needed to give the same yields as each component of a mixed crop growing on one unit, if they were, instead, grown as sole crops.

requires a degree of concern for the long term which immediate hunger and insecurities militate strongly against. Agroforestry seems to offer a way through this impasse by giving peasants more reasons to plant trees (hence the insistence of ICRAF (International Council for Research in Agroforestry) that only *multipurpose* trees should even qualify a system to be called an agroforest); and also by making it more likely that a farmer's title to his trees will be secure.

In designing an agroforest for a concrete situation, a very wide variety of aspects of that situation are relevant. ICRAF have stressed the importance of the stage of *diagnosis* which should precede that of design itself. Essentially this consists of identifying the criteria which an appropriate design must fulfil.

Diagnosis is followed by consideration of the ability of candidate designs to fulfil the diagnosed criteria. The intention of this work is to contribute to thinking about methodology for such evaluation in terms of approximate prediction of what would be the yield and loss risk for each component of a hypothetical mixed-plant 'community' if it were grown on given land under assumed management and climate regimes.

In the context of sole crops agronomists spend working lives finding answers to the equivalent questions for very many specific situations and yield trends gauge their effectiveness. There is, however, a gap in methodology when it comes to mixed-plant communities, and this is not accidental. The economic and theoretical problems of predicting the behaviour of the components and of systems containing them are formidable.

Field trials of tree species, as against annuals, take longer - often much longer - to bear results, require larger plots and much larger guard rows and are therefore more expensive. Each of these factors - time, space, and expense - effectively reduces the cybernetic *variety* which can be deployed experimentally by the scientist. In actuality for many of the trees proposed as candidates for agroforest systems, far from their having been observed under experimental conditions, we do not even have estimates of yield from farmers' fields. *E.g.* on ICRAF's Tree and Shrub Database out of a total of 505 records on 370 species only 161 gave any yield figures at all (von Carlowitz, 1986).

The number of possible agroforest systems (generated by choice of component species, spatial and temporal planting patterns and management regimes), and thus the *variety* which the scientist has to deal with, is really colossal. The pattern/process/structure of plant responses to environmental stimuli must be far more complex in a mixed stand than in a sole crop since their responses *to each other's* responses will not be homogeneous and therefore cannot be omitted from an effective understanding.

Interactions between neighbouring plants of different species or varieties are what generate much of the intractable complexity of multispecies crop behaviour, and for this reason I chose neighbour interactions as the area within which to carry out my research.

From a larger number of possible approaches on this theme of neighbour interactions three were chosen for investigation in this thesis. The three have in common that each is basic (rather than applicable to specific types of agroforest) and appears to be potentially useful to the field, but is not yet part of the normal repertoire of technique and theory available to agroforest science. Each approach involves experimental investigation of a different kind of spatial relationship. One deals with competitive interactions, one with a practical approach to quantifying interactions, and the other with cooperative interactions.

The first of these, Part I, represents an attempt to apply insights from theory on the ecological strategies, or 'functional types', of wild plants to the problems of designing efficient agroforest systems. I believe that Grime's C-S-R model of ecological strategies, if it can be mapped onto economic plants, may go some way to accomplish the task of *variety reduction*, enabling a typologising of interactions occurring between the neighbouring plants constituting an agroforest into a much smaller number of *types* of system. A specific prediction was made and tested experimentally that, when grown together with an understorey, a stress-tolerant tree's roots would occupy space in such a way as to interfere less than would those of a competitor tree with the roots of the understorey plant.

Part II represents, by contrast, a purely technical attack on the same problem. This is distance based neighbourhood modelling: a statistical method of *measuring* the effects which neighbouring plants have on each other, which has not yet been much applied to mixed cropping systems as opposed to wild plants. The method could, I thought, be extended to give us a way of optimising agroforest yields if it could first be applied to multispecies situations (meaning those with more than three species). My contribution is to show how the use of z-scores renders multispecies situations only slightly more complex than sole crops, and to indicate how an optimising method could be developed from a neighbourhood modelling basis.

Part III of the thesis deals with the possibility of the occurrence, and possible mechanisms, of cooperation between green plants. My attention had been drawn to the existence of carbon transfers between plants through connecting mycorrhizal hyphae in the early part of 1987 by J.P. Grime², who suggested that studies of interactions between plants could not safely ignore the phenomenon. At the time I could see no way that Agroforestry could take these factors into account, but if inter-plant cooperation does occur then it may

have considerable importance for agroforest design, since in wild plants, direct nutrient transfers apparently resulted in substantial differences in growth; and one might expect this to occur also in agroforests. Perhaps, also, cooperation between components of an agroforest could result in yield increases or some damping of yield oscillations and hence a reduction in economic risk.

I was puzzled and fascinated by the direct nutrient transfer findings which seemed to be utterly contrary to the current paradigm which holds that, apart from what might be termed incidental effects (such as one plant's olfactory defences against predation also benefitting a neighbour) the only significant interactions between neighbouring plants are competitive.

I studied theory on cooperation wherever I could find it. In the study of plant-plant interactions, literature in the three fields of 'biotic specialization', direct nutrient transfers and intercropping all contain results which are difficult to explain under the competition paradigm. The possibility of plant-plant cooperation ('mutualism') has been raised by several authorities as a result of work in biotic specialization (Aarssen & Turkington 1985; Thompson et al. 1990) as well as direct nutrient transfers (Grime et al. 1987).

There were well-developed ideas on cooperation in Game Theory, following the work of Axelrod and Hamilton (1981) on reciprocal altruism as an iterated Prisoner's Dilemma game, and these, with others, were being applied in animal evolutionary theory. Game theory seemed to lead to a clear prediction that cooperation should be *more* likely to occur in plants than in animals because plants are sessile. Yet the field was virtually empty, and I kept coming up against what seemed at first the insurmountable theoretical barrier that the existence of competition between plant neighbours cannot be doubted and must surely preclude cooperation.

Solving this problem by the use of a 'thought experiment', which purports to show that there is no reason why plants cannot compete and cooperate simultaneously over the same resource, opened the way to an application of cooperation theory from other fields to Plant Ecology. This begins with an approach to what I believe are significant gaps in theory concerning the nature of the mycorrhizal fungus-plant relationship itself, then moves out to consider the case of two plants connected by a mycorrhizal fungus. This thesis argues that the only possible basis for inter-plant cooperation to persist as an evolutionarily stable strategy lies in the existence of some 'decision'-making capacity whereby a plant which is faced with a situation containing the possibility of cooperation must have the ability not only to *cooperate* but also to *not cooperate*. Two experiments were designed and carried out to test a hypothesis based on this prediction.

² Botany Department, Sheffield University

This PhD research project, carried out with a research studentship funded by the Open University from The beginning of 1987 to the end of 1989, began with a theory of the ecological strategies of wild plants and the hope that this could be applied predictively to agroforest systems. It ends with the possibility that another, and different, kind of strategy is operated by wild plants, which, like ecological strategy, may have implications for agroforest systems. The method of neighbourhood distance modelling, which I worked with between these two, has possibilities of useful application to both of them.

PART I. APPLICATION OF GRIME'S MODEL OF PLANTS'
ECOLOGICAL STRATEGIES TO AGROFOREST SYSTEM DESIGN.
Chapter 2. Summary of Part I

Grime's C-S-R model of the ecological strategies pursued by wild plants is described. It constitutes a deep mine of concepts capable of application to agroforest - and other - ecosystems which are managed for production, yet remains virtually unexploited. A particular prediction which the model would appear to suggest is that *stress-tolerant* trees may interfere less with an understorey component than do *competitive* trees. Experimental results are presented which go some way to confirm one aspect of this prediction through looking at the different patterns of spatial occupation manifested by the roots of Holly as compared with Poplar, when grown with an understorey.

Chapter 3. Grime's C-S-R Model

Grime's (1974, 1977, 1979) theory describes and accounts for the ecological behaviours of different wild plants coherently and powerfully, in terms of '*ecological strategies*' and seems predictively very rich. He defined an ecological strategy as '*A grouping of similar or analogous genetic characteristics which recur widely among species or populations and cause them to exhibit similarities in ecology.*'

Grime suggested that *biomass* in any habitat is limited by factors in only two categories: *Stress*, defined as: '*limiting the production of biomass*'; and *Disturbance*, defined as: '*causing the destruction of biomass.*'

Permutation of these two categories at high and low levels yields four extreme types of habitat (see Table 1) of which only three are viable for plant life, since in a highly stressed and highly disturbed habitat stress will prevent the re-establishment of vegetation after disturbance.

In each of these three habitat types, plants evolve a distinct adaptive *strategy*.

Table 1: The three extreme habitat types and ecological strategies which correspond to them.

Intensity of Disturbance	Intensity of Stress	Strategy name	Symbol
low	low	Competitive	C
low	high	Stress-tolerant	S
high	low	Ruderal	R
high	high	(no viable strategy)	

Grime (1979) suggests that the essences of the different strategies may best be grasped by looking at, and understanding the reasons for, their different responses to stress.

Stress-tolerant Strategy evolved in undisturbed habitats of intrinsically low productivity. Since such intrinsic stresses cannot be avoided the plant must *tolerate* them by having low resource requirements. Roots and leaves must be long-lasting; the root/shoot ratio changes only slowly and slightly in response to increasing stress; and metabolic activity may decrease to very low levels.

Ruderal Strategy evolved in potentially productive but highly disturbed habitats. A ruderal plant responds to the onset of stress by rapid curtailment of vegetative growth and switching resources into accelerated seed production since, in its natural environment, stress - e.g. drought - may be a prelude to disturbance - e.g. severe drought.

To the extent that stress intrinsic to the environment and disturbance are absent, stress will develop as a result of *competition*, defined as '*The tendency of neighbouring plants to utilize the same quantum of light, ion of a mineral nutrient, molecule of water, or volume of space.*' (Grime, 1977).

Competitive strategy thus evolves in highly productive and undisturbed habitats such as forest gaps left by tree falls. Stress experienced by a plant growing here develops as a result of the competition of its neighbours - *e.g.* for light. The plant responds to this stress by reducing reproductive effort and throwing all available resources into rapid growth to *escape* the stress - *e.g.* by growing higher than its neighbours.

Note that there can be no escape from stress which is intrinsic to a habitat since there is nowhere to escape *to*; whereas escape from competitive stress *is* an option. Hence the difference in evolutionary responses to intrinsic and competitive stress. Table 2 lists some salient attributes of the extreme, or 'primary' strategies. Most plants do not exhibit the extreme strategies, but fall at some intermediate point between them. The three extreme strategies may be represented as the vertices of an equilateral *ordination triangle* (whose sides are the vectors of intrinsic stress, disturbance and competition). Any individual plant's strategy may then be represented by the position of some point within this triangle. Such a point has three coordinates - one for each side of the triangle - of which the magnitude of any two determine the third (since competitive stress develops to the extent that intrinsic stress and disturbance are not present).

Grime's schema is not the first. MacArthur and Wilson (1967) produced the first widely used ideas of ecological strategy. Their categories of *r*- and *K*-selected strategies correspond closely to Grime's 'R' and 'C' respectively. Southwood (1977) is another synthesis from the realization that a third strategic extreme is needed where resources are poor. He terms this 'adversity-selected' strategy (which Greenslade, 1983, abbreviated to 'A-selected strategy'), and again it corresponds well with Grime's 'S' category. The axes, however, into which he resolves the factors determining selection type are not identical with Grime's stress and disturbance levels. Southwood's habitat favourableness may be equated (given a change of sign) with Grime's stress; but in place of disturbance, he employs the slightly imponderable concept of habitat *predictability*.

Table 2. Some characteristics of the extreme strategies

Name of strategy	Competitive	Stress-tolerant	Ruderal	--
Symbol	<i>C</i>	<i>S</i>	<i>R</i>	
Natural habitat	undisturbed, productive	undisturbed, unproductive	disturbed,	
Maximum vegetative growth rate	high	low	high	
Seeds as fraction of D.M. production	low	low	high	
Lifespan of plant	long	very long	short	
Longevity of leaves and roots	short	long	short	
Max. sink strength of roots for soil nutrients	high	low	high	
Luxury consumption of any excess nutrients	low	high	low	
Resource uptake and use times	strongly linked	often de-linked	strongly linked	

taken from Grime (1977) and Chapin (1980)

Chapter 4. Implications of Grime's Model for agroforest components

Domesticated plants have been selected for different qualities than have wild plants - for high or reliable yields rather than survival. Could the model therefore be valid for wild plants but not for those which have undergone intensive selection by man? My feeling is that the genetic linking described above is probably quite strong enough to persist significantly against such selection pressure even for plants which have been artificially selected for many generations (ancient annual crops). As regards tree species, however, no artificial selection has taken place in many cases (von Carlowitz, 1986) and in the remainder the number of generations affected must be far fewer than for annual crops. It appears worthwhile to proceed cautiously with an attempt to apply Grime's model to ecosystems managed for production, but to recognise that any predictions generated will have to be tested experimentally before they can be accepted.

4.1 Plants for Situations of Low Fertility:

According to the model one may expect that different degrees of stress-tolerance would be most suitable for sites having different stress levels. A research station in the tropics is usually sited on fertile soils whereas many of the farmers it seeks ultimately to serve are not - especially those likely to be targeted for Agroforestry solutions. Two of the characteristics of stress-tolerance are low growth rate and high luxury consumption³ of excess nutrients. In variety field trials there is therefore a risk that the wrong (least stress-tolerant) varieties are selected for use in infertile sites because they behaved efficiently on the research station.

4.2 Strategy and breeding for particular characters:

Plant strategies are expressed through 'functional balance' - the plant's allocation of captured resources between different functions in such a way as to maximize the genome's probability of survival and increase. Only certain patterns of allocation will *ever* be thus adaptive and only a range of these will be adaptive for a habitat with given degrees of intrinsic stress and disturbance⁴. Through evolutionary time (and space) the genome line is likely to have to adapt repeatedly to different levels of intrinsic stress and disturbance as it persists through climatic cycles or peregrinates through different types of land over the

³ 'Luxury consumption' is a misleading term here since the 'S' strategist is actually laying up stores of nutrients in excess of immediate requirements which may be used later when needed. Whether such a trait happens to be useful or deleterious to the farmer would depend on the environmental and management regimes.

⁴ The degree of competition is determined by these and can therefore be left out of account here.

generations. There is good evidence for this being a frequent occurrence in the finding that often even different races within the same species exhibit substantially different strategic behaviour (Grime *et al.*, 1988). Therefore the various characteristics which interlock *functionally* to form a strategy are likely to have become *genetically* interlocked since those allocation patterns not conforming to *any* coherent strategy would *always* be selected against. Perhaps it is advantageous for genome lines to retain unexpressed adaptations to previous climatic conditions, which will facilitate evolutionary responses when climatic change occurs.

For this reason the breeder should expect to find it more difficult to breed for combinations of qualities not characteristic of any one strategy. He is likely to find that breeding for a ruderal character (say) such as high and early seed yield will entrain other ruderal characters such as relatively good reproductive yields in years when stressful conditions develop towards the end of a growing season, but also early yield decline and senescence. To take another example, it could be argued that the main thrust of plant breeding is away from stress-tolerant character (and towards high seed or timber yield) whilst piecemeal attempts are made to breed back resistances to particular pests and diseases - a stress-tolerant character. Perhaps this might explain why such resistances so often prove short-lived.

4.3 Implications for interactions between agroforest components

It may be as well to state, before going any further, that Grime is *not* saying that all intrinsic stresses are equivalent. A plant adapted to drought stress is not likely thereby to be fitted to deal with the stresses associated with waterlogging, and so on. It will of course be necessary to match the specific environmental (and managerial) constraints operating over a proposed agroforest to the specific capabilities of particular plants - to tolerate an alkaline soil, survive heavy browsing or whatever. Nevertheless the model does seem to be a rich predictor of the ways in which agroforest components could interact. Here are a few examples.

a) A (relatively) 'R' tree⁵ below a 'C' tree: could yield highly in precisely those years in which the 'C' tree does poorly, by responding to stress with increased reproductive effort as a proportion of total resource use.

⁵ One needs to be careful in talking about ruderality in trees. Grime (pers. comm.) decries the term 'ruderal tree' as a contradiction in terms, since all trees' positions in the ordination triangle are far from the ruderal corner. I feel it is nevertheless useful to recognise that some trees are more ruderal than others, and that their ruderality may be important in terms of their behaviour, even though its degree may be slight in comparison with that of any annual plant.

b) A 'C' tree above any component: is likely to be harmful to it unless planted at wide spacing or pruned or both due to the high level of competition for resources which it exerts.

4.4 Allelopathy

Allelopathy should be expected in 'S', rather than 'R' or even 'C' strategists. Although very hard to demonstrate conclusively as either present or absent and therefore likely to pass unrecognized, it may be an important type of interaction in nature (Rice, 1974, 1979). It could also have importance in agroforests both negatively - as reducing production; and positively - for example as enabling us to isolate the individual root systems of an agroforest component species from each other with an intervening component which is allelopathic to it. This would be useful as a way of controlling underground spreading of pests and diseases from one plant to others.

4.5 Complementarity and Nutrient Efficiency of Agroforest Mixtures with 'S' vs. 'C' Trees

In Agroforestry literature, one often comes across the idea that a tree component can be expected to recover nutrients which would be lost, or not used, by an annual component. I want to suggest that, as regards such *complementarity*, the behaviour of a 'Stress-tolerator' ('S') tree, as against that of a 'Competitor' ('C'), should be very different.

An 'S' tree above an ('R') annual crop could retrieve nutrients which are available at times when they could not be used by the annual (e.g. 'Birch effect' nitrogen at the beginning of a rainy season). It would show less tendency than a 'C' to immediately utilize these in growth, being more likely to store them as a reserve against hard times. An 'S' would not compete with the 'R' for nutrients so fiercely as would a 'C'. The root system of an 'S' might tend neither to grow much into soil volumes occupied by the 'R', nor to colonize these same volumes rapidly when the 'R' was not there (after harvest). It might be more likely, if it were possible in a particular soil, to grow below the 'R's rooting depth where its roots would not be competing with the 'R's, but recovering nutrients lost to the latter. Any disturbance due to cultivations would tend to reinforce such a pattern as an 'S' strategist would not rapidly recolonise its lost rooting space in the cultivated layer. In cases where the two components' root systems coincide in time and space the 'S' might reduce root metabolic activity there until resources were again available at a higher level. To sum up, when and where the annual component exerts competition for resources, an 'S' plant should compete least.

A 'C' tree in association with an 'R', on the other hand, should compete more for nutrients and/or water, and show a greater tendency to immediately invest captured resources in vegetative growth, both above and below ground, thus increasing its competitive dominance. Management in the latter case may therefore have to try to limit

the deleterious effects of competition by the 'C': perhaps with wide plant spacings, cutting of branches, pollarding, thinning or, possibly, selective fertilization.

Chapter 5. An Experiment

An experiment was designed to test the prediction that a contrast should be found between a stress-tolerator and a competitor tree when each is grown with the same (agriculturally) annual understorey.

The predicted behaviour of root systems in an 'S'/'R', as opposed to a 'C'/'R' plant association (observable through clear perspex walls), is as follows. More than the 'C's, the 'S's root system will avoid competition with the 'R's by its pattern of spatial occupation. I.e. the proximity of living 'R' roots will lessen the probability of tree root growth occurring in a given soil volume more in the case of an 'S' than a 'C' tree.

It was hoped to answer, from the same experiment, the further question does the 'C's root system even concentrate growth in volumes contested by that of the 'R'.

5.1 Materials and Methods

Root Observation Chambers: Root observation chambers were constructed from tea-chests 60 cm high, 50 cm long and 40 cm wide. The 60 cm X 50 cm sides were cut out, except for a 5 cm margin all round, to allow 4 mm clear perspex sheets, scribed with a 2 cm grid on the inside of the perspex, to be set in. The bottom of each chamber was reinforced with ferro-cement consisting of 7 layers of 5 cm mesh chicken wire reinforcing 2:1 sand:cement mortar. This ferro-cement floor was not flat, but smoothly graded down to a 3 cm drain hole in the centre. Wood surfaces were treated inside and out, before construction of the floor, with three coats of household water-tank paint, this being thought less likely to affect plant growth than other types. The cement surface was similarly treated. Light had to be excluded from the observation windows, to avoid its affecting root growth or, more important, allowing a growth of algae on the inside of the perspex, which would have obscured vision. Black polyethylene sheet was fixed across each window, taped to the box down the left side and 'buttoned' with elastic loops round screw-heads on the right, to allow easy removal and re-fixing.

The root observation chambers were housed in an unheated greenhouse set up on bricks in a row 30 cm apart, and filled with a 50:50 mixture of a loamy sand soil and sharp sand, previously riddled and homogenised.

Treatments: Three replicates of two mixed systems, designed as models of agroforest systems, were to be compared. In both cases a tree was grown with Beetroot (*Beta vulgaris* L., variety Dwergina - a fast-growing 'babybeet'⁶) as an understorey component. The reason for using beetroot was that its roots, being crimson, are easily and unequivocally

⁶ from Cramphorn Ltd., Chelmsford, Essex. Supplier's reference no. 2144.

distinguished from those of other species. For the overstorey plants Lombardy Poplar (*Populus nigra* L., variety *Italica*) was chosen as the Competitor strategist, since it is fast growing. For the Stress-tolerator Holly (*Ilex aquifolium* L.) was chosen as a compromise: it has quite stress tolerant character in that it grows slowly, is small, and has shiny, evergreen leaves which are defended against predators. Choice of a more extreme 'S' strategist, such as Yew (*Taxus baccata* L.), would have introduced a risk that its roots might grow too slowly to give useful data within the lifetime of the experiment. The trees were bought from a local nursery as whips. Other treatments were also set up but are not dealt with here.

Randomization and Blocking: The trial was divided into three blocks, each containing one plot of each of the treatments. Treatments were assigned positions in the blocks using a random number table.

Establishment: Advice was taken that holly roots grow slowly and might even never reach the observation soil volume; it was therefore decided to plant each tree near (15 cm from) a corner of its box. This was done on 13th May 1987. After 4 weeks, when it was clear that the trees had survived transplanting, beetroot seeds were sown 2 cm apart in drills 2.5 cm deep. These were arcs of concentric circles with radii 12.5, 25 and 37.5 cm centred in the tree stem at soil surface level.

Observations: Positions of roots growing against the perspex at the end of the experiment were recorded, between March 21st and March 25 1988, by location and species wherever they intersected a line of the grid. Other observations were also made but are not dealt with here.

5.2 Statistical Treatment

Positions of roots intersecting grid lines were transferred from the recording sheets to data array files in a computer - a separate array for each species' roots in each box. A Pascal program was written and used to calculate, for each box, numbers of 2 cm grid line elements having:

- a) no intersections with roots
- b) intersections only with roots of the tree component
- c) intersections only with roots of Beetroot
- d) intersections with both Beetroot and tree roots

Multiple intersections of a single species' roots with one grid line element were treated as simple (single) presence. Data and programs written are presented in appendix 3.

The resulting numbers of intersections were subjected to Chi-squared analysis, detailed in Table 3, to test the two, separate hypotheses that:

- a) Holly roots coincide with Beetroot roots less often than would be expected on random assumptions, whereas poplar roots do not; and
- b) Poplar roots coincide with Beetroot roots more often than would be expected on random assumptions.

Table 3. Observed and Expected frequencies of root intersections with 2cm grid line elements.

HOLLY AND BEETROOT				
(Totals of Boxes 1, 9 and 13)				
B e e t	-	Holly		Total
		-	+	
		701	42	743
		713.6	29.4	
	+	440	5	445
		427.4	17.6	
Total		1141	47	1188
ChiSq =		0.22 + 0.37 +	5.41 + 9.03 =	15.03
df = 1		Significant at P < 0.001		

POPLAR AND BEETROOT

(Totals of Boxes 5, 8 and 14).

		Poplar	Total	
		-	+	
B e e t	-	560	68	628
		563.5	64.5	
	+	506	54	560
		502.5	57.5	
Total		1066	122	1188
ChiSq =		0.02 + 0.02 +	0.19 + 0.21 =	0.45
df = 1		Not significant.		

These results are consistent with the hypothesis that Holly roots coincide with Beetroot roots less often than would be expected on random assumptions, whereas Poplar roots do not. The magnitude of the effect is considerable. Only 5 Holly roots coincide with Beetroot roots whereas 17.6 are expected; while 42 are found not coinciding as against 29.4 expected.

Poplar roots, on the other hand, coincide with Beetroot roots almost precisely as often as would be expected on random assumptions.

5.3 Discussion

Up until the 1950s or 1960s western experts deprecated the annual intercrops in tropical farmers fields as inefficient and unproductive. This assessment was able to persist because intercrops were simply too complex for Modern Science to deal with at that time. Perhaps Modern Science is less haughty today; at least it does not rubbish agroforestry practices. Yet, despite the (last, desperate) hope of maintaining land fertility which Agroforestry holds out, in the face of the colossal cybernetic variety of agroforest systems work on design proper, (as opposed to *evaluating* simplified variants of the designs arrived at by peasants) is wanting because of the lack of a sufficiently powerful variety filter. The C-S-R model, as a 'tool to think with', may be such a filter, extending the promise of a way of *typologising* agroforest component species/varieties in ways that may allow us to understand what types of plant are suitable for what land types (the nature of stress-tolerant character being especially important here); and also what effects different types of plant are likely to have on each others' behaviours within a mixed system.

Further research needs to quantify to what extent coherent ecological strategies persist in genotypes that have undergone artificial selection. Beyond this a whole new systematic approach to understanding complex managed production ecosystems is waiting to be built.

PART II: THE USE OF Z-SCORES IN A DISTANCE BASED
SPATIOTEMPORAL DYNAMIC MODEL OF INTERACTIONS
BETWEEN PLANT NEIGHBOURS: A STEP TOWARDS OPTIMISATION
MODELLING OF PLANTING PATTERNS AND SPECIES MIXTURES IN
AGROFORESTRY

Chapter 6. Summary of Part II

Interactions between different annual species planted as intercrops have been studied routinely to good effect using replacement series field trials and analysing results to give Land Equivalent Ratios (LERs - also known as Relative Yield Totals), the great advantage of which is that they provide a valid basis to treat yields of different species together. However, there has been little investigation of interactions between neighbouring trees of different species, to date, since the same method, although useable in principle, would require too much experimental resource to be practicable.

Measures of local interference at the level of the individual plant have been in experimental use since Goodall (1960) to explain variance in plant growth parameters. These methods, individual plant-based rather than population-based, appear to offer some promise for the study of tree-tree interactions; but the fulfilment of this promise has been hampered by two factors: the small fractions of variance often explained by these methods, and the lack of a way to treat the yields (etc.) of different species on a common basis.

If the problems can be overcome then analysis of local interference methods have the potential to offer a firm basis for the design of optimized plant production systems of any type.

The present work suggests and illustrates a solution to the problem of finding a common basis for yields of different species in a mixture which is borrowed from the field of anthropometric evaluation of malnutrition in human populations: the use of z-scores.

An experiment is described in which a six-species mixture was planted on random coordinates, employing annual and biennial plants as 'model trees' since real trees would have taken too long to yield results.

Heights of the plants were measured at intervals, and fresh weights at harvest. These data (and height growth rates derived from them) were then regressed on six 'neighbourhood predictor' parameters calculated only from the location coordinates of all the plants in the plot, intended to estimate the extent to which a plant was neighboured by each of the six test species.

Chapter 7. Introduction

It has become apparent from intercrop experiments that large yield advantages often result from growing two annual plant species together instead of separately, probably in most cases because of complementary resource use (Willey, 1979). How can we choose the best such systems? The quantity used to analyse the effectiveness of a mixed crop trial with annual species is the Land Equivalent Ratio (LER). The LER of each component of the mixture is the ratio of its yields per unit area when grown in the mixture and when grown as a sole crop. The LER of the mixture is the sum of all its components' LERs. Thus the mixture's LER has the meaning how much more land would be required to give the same yields of each component if they were grown as sole crops. An $LER > 1$ signifies it is advantageous to grow the mixture; an $LER < 1$ that the mixture is disadvantageous compared to sole crops.

Rao and Willey (1983) used a strip-plot design in which parallel strips of different crops (and of no crop) are randomized orthogonally across each other: an efficient design, in which many systems may be tested at once. Nevertheless, the number of possible two-species intercrop systems is large enough to constitute very much work even for annual crops needing only a few months' experimental resources.

In the case of mixtures including tree species the large plot sizes and wide guard rows, together with the long time-scales which would be required to calculate LERs (Huxley, 1983a), have meant that we have not been able to experiment on tree-tree interactions in this way, and mixed-tree cropping has not become a subject of academic study in the way that first intercropping and then tree-understorey interactions in agroforestry did. Nevertheless, there seems every reason to expect that yield advantages may be gained by growing the right combinations of tree species in mixed systems for timber production.

In agroforests also, trees are often located close enough together to be interacting with each other. In either of these situations knowledge of which tree-tree interactions are most economically beneficial would almost certainly be profitable.

7.1 Distance models of plant/neighbour interactions

Plant ecologists use analytic or neighbourhood spatiotemporal dynamic models to investigate spatial processes acting on plants, and these are schematized by Czaran and Bartha (1992) and by Benjamin and Sutherland (1992). There are two analytic types - Reaction-diffusion models and Patchy-environment models. Both arose from the need of animal ecologists to show that spatial processes operate on animal populations, and both have since undergone some, limited application to plants. An analytic model is applied at

the level of a population and has the advantage of possessing an exact, mathematical meaning, but the disadvantage of treating space only as an average quantity (Ellison *et al.*, 1994) and of being difficult for non-mathematicians to understand (Ives, 1995).

Neighbourhood models use computer simulation and fall roughly into three types, based on the ways they define neighbourhood: cellular automaton models, tessellation models and distance models. All three were developed to deal with plants, and can be used to model at the level of the individual.

Cellular automaton models represent space in a rudimentary way via the cellular grid, the neighbourhood of a cell consisting of a zone of cells adjoining it.

Tessellation models, usually representing single-species situations, are rather more powerful in their treatment of space. They specify the resources available to the population as being represented by the planar surface in which individuals are spatially located as points, and define the parcel of resources available to an individual plant by dividing up the surface into polygons (one belonging to each individual), for example by including in one individual's polygon all those points which are nearer to it than to any other individual (*e.g.* Watkinson *et al.*, 1983). The neighbourhood of an individual consists of the set of individuals with adjoining polygons.

Aguilera and Lauenroth (1993) extend this approach by representing each individual by the shape of its basal area rather than by a point. Instead of a geometric formulation they then determine the polygon enclosing all points nearer to one plant than to any other by a Geographical Information Systems (GIS) method: allowing the boundary of each basal area shape to grow outwards by one raster cell at a time. When two boundaries meet they stop growing at their interface.

Distance models, as the name suggests, base their various definitions of an individual's neighbourhood on the distance to each neighbour, as well, often, as other parameters such as neighbour size.

Some distance models simply define an individual's neighbourhood as including all plants within a certain radius (*e.g.* Duncan, 1995; Pacala and Silander, 1990); but, such approaches, which treat distance as a boolean variable⁷, have proved inaccurate at the individual plant level (Mou *et al.*, 1995).

More commonly, distance models seek to embody the simple idea that a plant should interact more strongly with nearer or larger neighbours than with more distant or smaller ones (Goodall, 1960; Mack and Harper 1977; Cormack, 1979; Ellison *et al.*, 1994; Duncan 1995). In this type of pairwise distance model, in which distance is a continuous variable,

assumptions about the mechanisms of plant-neighbour interactions are easily incorporated. One type also draws circles round each individual, but then assumes interference between a focal plant and another is proportional to the extent their two circles overlap. This may suffer still from some artificiality in the assumption that interference is equivalent whether in the central or peripheral regions of such a circle.

Some workers have partially addressed this problem by drawing more than one circle and giving more weight to interference in an inner circle than in an outer (e.g. Mack and Harper, 1977; Bergelson, 1993); however one would expect interference to vary more smoothly than this with distance from the focal plant. Avoiding this difficulty, an inverse function of distance is commonly used whereby interference by each neighbour is inversely proportional to some simple function of its distance from a focal plant (e.g. Silander and Pacala, 1985; Benjamin and Sutherland, 1992; Brisson and Reynolds 1994).

Mack and Harper (1977) suggested that relative success of an inverse distance cubed model in explaining variation (e.g. Goodall, 1960; Ross and Harper, 1972) implies that competition is occurring in three dimensions: for example for light, or for soil-borne resources at depths which depend on plant size (e.g. plants with tap roots). By implication, success of an inverse distance squared model would connote that plants are competing as if two-dimensionally - *i.e.* for resources whose availability is proportional to the plant's lateral occupation of space.

This could be because root systems' depth is constant from some time soon after establishment so that competition, although not actually two dimensional, does not vary with depth differently in different plants, allowing depth to be ignored in the interference model. Alternatively root systems may avoid interpenetration, or rosettes stop lateral growth when they touch a neighbouring rosette; and in these cases the effects observed may be seen as due to avoidance of competition (e.g. Duncan, 1991), rather than of competition itself. Since the earlier papers in the field, not much attention has been paid to this aspect of the meaning of the power index to which distance is raised in distance models. An inverse square model is, however, more frequent in the current literature.

In monocultures, distance models have been used mainly to address the $3/2$ power self-thinning law and population size structures, while in multi-species situations they are employed to study population ecology (Czaran and Bartha, 1992).

Because it violates the requirement of regression analysis that predictor and response variables must be statistically independent of each other, use of neighbour size (which is

⁷ That is, a variable taking values only of either zero or one.

common) in a distance model overestimates the degree of correlation if more than one plant in a stand is treated as the focal plant (Firbank and Watkinson, 1987).

Despite this, work with neighbourhood models has suffered the problem that neighbour interference often explains little of the variance in plant parameters under study, except, interestingly, in the case of dune or desert plant communities⁸ (Cormack, 1979). Firbank and Watkinson (1987) noted that about 20% of variance in individuals' yield could typically be attributed to neighbour interference. Bergelson (1993) examined 100 cases from the literature up to 1987, finding, similarly, a median R square of 0.21. Firbank and Watkinson (1987) used a distance model for a two-species mixture. Their model accounted for less than 10% of the variance in their own data. It is particularly interesting that they report regression on emergence time and the same neighbourhood model as able to account for only similarly small proportions of yield variation when applied to *computer simulated* data in which these parameters were known to be the only ones present. Several reasons have been proposed for the generally poor fit of distance models, and the resultant elaboration of the methods used has improved this (Ellison *et al.*, 1994).

Thomas and Wiener (1989) pointed out that previous distance models assumed competition to be two-sided even though it was believed that competition is often one-sided or at least asymmetric, for example because of overtopping. They therefore suggested that inclusion of competitive asymmetry in distance models should improve their fit; and proposed, and applied, a measure of competitive asymmetry in which the effects of neighbours smaller than a focal individual are discounted by a constant factor. Duncan (1995), however, drew attention to a fault in their method which will lead to a spurious conclusion that competition is asymmetric if plant size correlates with performance (which it has been found to do) because discounting increases the correlation between size and the measure of interference.

Time or rank order of emergence, it has been suggested, is one source of variation in individual plant performance that is often not included in neighbourhood models and which can improve the fit of models (Firbank and Watkinson, 1987; Bergelson, 1993).

Angular dispersion of neighbours has been put forward as another source of variation worth investigating (Czaran and Bartha, 1992); and Bergelson (1993) suggested, in addition, that a neighbour's interference effect on a focal plant should be expected to be reduced if a third plant is located between the two. Her experimental results may or may

⁸ That is to say in high stress environments. It is somewhat ironic that the best evidence for 'competition' between individuals has thus, apparently, come from stress-tolerant species.

not vindicate this view⁹. However, as she points out, her method is very restricted in applicability. Bergelson sowed 3 different densities of competitor in each of three concentric bands around the focal plant then included these densities as categorical variables in an ANOVA analysis, interpreting statistical interactions between band densities as indexing 'interaction between competitors'¹⁰.

Benjamin and Sutherland (1992) suggested that in some situations models which assume that the efficiency of resource assimilation has circular contours are inaccurate because plants respond morphologically to the spatial patterns of resource availability. This must be especially true below ground, root morphology being more plastic than shoot morphology. Brisson and Reynolds (1994) explored this problem, excavating the root systems of 32 creosotebush plants growing together. They drew a closed angle polygon to enclose each root system. The degree of overlap of these polygons (4%) was much less than that of circles centred on each stem and of area equal to its polygon (20%). Clearly these root systems were behaving in such a way as to avoid overlapping each other. They also calculated competitive pressure vectors by (amongst alternative methods) integrating a vector from each neighbour of magnitude equal to the inverse square of its distance from the focal plant, and of direction equal to that from the neighbour to the focal plant. There was a strong correlation ($P < 0.001$) between this vector and the main direction of root

⁹ She reports only that a dispersal estimator for competitors and a ranked estimator of focal plant's emergence time *taken together* improve the fit of model.

¹⁰ She is pessimistic about the possibility of developing a more widely applicable method: 'while this made analysis of my experiment simple, it remains to be seen how the interactions-between-competitors can be described for the wide variety of patterns that would be found under natural field conditions. It is even harder to envisage how these interactions can be incorporated into models of plant population dynamics. While these difficulties make the interactions-between-competitors no less important, they may make it impossible to describe adequately the competition between plants for many species.' What is required here appears to be a geometric method for modelling the extent to which a competitor is occluded from the focal plant by intervening plants. This must be possible. For example:

Consider a focal plant P at distance d_i from C_i , the 'competitor of interest'. P is also at distance d_o from C_o (another competitor). C_i and C_o subtend an angle r at P and have size m_i and m_o respectively. Then the occlusion effect can be crudely represented in, for example, a sum of reciprocal distance squared model by an occlusion coefficient OC (which would be used to multiply the $1/d^2$ term before summing) thus:

$$\begin{aligned} OC &= \sin(r/2) \times d_o/d_i \times m_i/m_o \\ &= \sin(r/2) d_o m_i / m_o d_i \end{aligned}$$

or, if it is not desired to take size into account:

$$OC = \sin(r/2) d_o / d_i$$

growth (defined as that from the stem to the centroid of the polygon). Inclusion of neighbour size in the competitive pressure vector did not improve fit.

Either of two conceptual models, which they were not able to choose between, could have explained their findings. Both assume that two root systems either cease growing or slow their growth in any zone in which they meet; the difference between them being that in one model compensatory growth will occur elsewhere, whilst in the other it will not. A split root experiment of my own (Eve, unpublished), in which barley plants were each allowed to grow roots into soil-packed tubes at two of four different levels of penetrability, showed that compensatory growth was occurring, and I suspect that it may be common in other species.

Mou *et al.* (1995), working with a mixed stand of Sweetgum (*Liquidambar styraciflua* L.) and Loblolly Pine (*Pinus taeda* L.), similarly found that root systems tended to avoid overlap and that the two species' root systems did not behave in the same way, concluding that distance models should incorporate modular growth simulations of root growth based on further studies of root system architecture, since assumptions of symmetrical root systems appear to be invalid in many situations.

Benjamin and Sutherland (1992) suggested that different species and situations are probably best fitted by different neighbourhood models, substantiating the claim experimentally. They posit this as the reason for the persistence of a variety of models in the literature and recommend a diverse and flexible approach to choice of models. Since plants work in different ways this seems a logical approach.

However it may give rise to a problem, in that different neighbourhood models may be appropriate for different species even within the same experiment. How could this be accomplished? Transformation of interference coefficients to their z-scores would appear to offer the possibility of a simple way of incorporating unlike sub-models together, with the additional advantage, from the viewpoint of statistical validity, that the resultant distributions are always normal.

7.2. Aims

When I began this work in 1987 I was unable to find individual based distance models dealing with multispecies interactions (meaning more than two species). Gross *et al.* (1992) were aware, still, of 'very few' of these; and pointed out that there were serious difficulties involved in multispecies modelling - especially of spatial and temporal scale. Plant communities may present less of a problem than animal communities in this respect; nevertheless most individual based modelling of plants has dealt only with single species

(DeAngelis and Gross, 1992). Ford and Sorrenson (1992) similarly described such modelling as recent.

My first aim in this section, borrowing an idea from treatments of human population size structure, is to demonstrate the usefulness of z-scores for individual based models, with which a multispecies model becomes little more more complex than a single species one.

Distance models have so far been preponderantly of wild plants and little work has been done with economic plants, especially mixtures. In wild communities, the thrust of modelling is to gain ecological understanding; but in economically managed ecosystems the objective of modelling will, rather, be to optimise production.

My second aim is contribute to the eventual development of an optimization method suitable for mixed cropping designs including trees. To this end I will describe how such a method might work, based on regression data from a distance model such as that presented here.

7.3 The use of z-scores

The z-score of a sample datum value is its difference from the sample distribution mean expressed in standard deviations, and is obtained for a sample observation by subtracting the sample mean and dividing the result by the sample standard deviation. Z-scores possess the useful property of always having a normal distribution with mean zero and standard deviation equal to one. They are often used to 'standardize' a sample distribution to conform to the common statistical requirement that sample data be normally distributed.

What suggested their use in the present context was an examination of the way anthropometric data are used to estimate the extent of malnutrition from the size structure of human populations. Here, they allow sample data of weight and height for children of different age and sex to be treated in aggregate. Using raw weight data would mean that such an estimate had to be carried out separately for each of several even-aged samples drawn from the population since, obviously, a weight that corresponds to a condition of malnutrition in one child may indicate normal nutrition in a younger child. On the other hand if each child's weight is expressed as a 'z-score'¹¹ then a value of, for example, -2 means that the child is among the smallest 5% of its age group, regardless of what its age

¹¹ I should, perhaps, point out that what anthropometrists term a child's 'z-score' is not one, strictly speaking. Rather it is what *would* be the child's z-score *if* he or she were a member of a 'reference population' of a large number of children drawn from the US or Europe. This does not materially affect my argument, however.

is. Statistical analyses can be performed on data from a mixed age (and mixed sex) sample provided the z-scores are used in place of raw data (UN, 1990).

The use of z-scores for dependent variables thus allows unlike data to be dealt with together in a regression equation. In the same way, using z-scores of a measure of focal plant performance, instead of the performance measure itself, will allow data on focal plants of different species to be entered together into a regression as dependent variables. Z-scores can also be used to allow unlike *independent* variables, for example interference coefficients of different species of neighbour, to be similarly aggregated in a regression.

In neither of these cases is it necessary to lose the species-specific information contained in data, since species can still be entered into the equation as one or two sets of dummy variables.

Using z-scores for both dependent and independent variables in a regression confers on B, the regression coefficient, units which have the meaning *the number of standard deviations of difference in the dependent variable associated with one standard deviation of difference in the independent variable*.

Chapter 8. A multispecies experiment analysed using z-scores

An experiment was carried out to test the feasibility of using z-scores in regression analysis of data from a mixed planting of six species of different habits. Ideally, data from a mixed tree species planting would have been used for this, since it is for trees that I envisage the method being most useful. However, such a trial would have needed a considerable area of land and time to carry out. No obvious reason was apparent why the method should work very differently with data from trees as opposed to other plants, however. The data were only needed to test the method, not to come to any specific conclusions about the behaviour of particular, or indeed any, species of plants. It was decided to go ahead with a 'data production system' employing five horticultural plants and a weed species as model trees, and repeated height measurements were taken as surrogates for the height and diameter at breast height data that real trees would have given.

8.1 Method and materials

Five garden varieties and a weed species were chosen for investigation: Leek (*Allium porrum* L., variety Musselburgh), Beetroot (*Beta vulgaris*, variety Dwergina), Creeping buttercup (*Ranunculus repens* L.), Marigold (*Calendula officinalis* L., variety Indian Prince), Broad Bean (*Faba vulgaris* Moench., variety Sutton) and Endive (*Cichorium endivia* L., variety Batavian Broad-leaved). Three plastic tanks of dimensions 107 by 52 by 50 cm depth were filled with sandy loam soil on July 22nd 1988. Each tank was planted in a different pseudo-random planting pattern with twelve individuals of each of the six species.

This was done using a list of uniform pseudorandom numbers generated by the MINITAB statistical package. Each successive triplet or pair of numbers was either used to determine, alternately, an x- or y-coordinate or discarded if it fell beyond the range $0 \leq x \leq 52$ or $0 \leq y \leq 107$. A seed of each of the six species was located thus in turn for each of twelve locations. An example of the resulting pattern (that for Box 1) is illustrated in Figure 1.

Buttercup was planted as a recently rooted ramet cut from a wild-growing plant and the other five species were all sown directly as seed. Each plant was identified by box, x- and y-coordinates and species; and plant heights were measured and recorded at intervals after first measurement of 7, 14, 21, 28, 36, 43, 50, and 67 days.

The method of measuring heights was as follows. For each box a datum plane was defined by the tops of the four sides. The lower side of a straight edge was placed across the box on the datum plane next to a plant being measured, and the measurement taken

from the datum plane to the top of the plant. In order to derive heights above the soil surface from these measurements, the height of the datum plane above the soil was measured at 18 points in each box. These datum heights were then processed by the UNIRAS UNIMAP package to give a contour map of the soil surface of each tank, and datum heights interpolated for each plant location. These three maps are reproduced as Figures 2 to 4.

Broad Bean plants were harvested, and weighed within ten minutes at 36 days because they had grown so large that it was feared they would dominate the experiment and obscure any effects of other species. The remaining five species were harvested and weighed within ten minutes of harvest at 67 days.

8.2 Treatment of data

Neighbourhood predictor variables were calculated for use as independent variables in the regression equations with the various parameters of plant performance. Both independent and dependent variables were standardised before use in the regressions.

8.2.1 Estimates of interference

Neighbourhood predictors - estimates of the interference caused to a focal plant by each of the six species of neighbour, which I will call '*interference coefficients*' (following Ellison *et al.*, 1994), were calculated using a program written for the purpose in PASCAL (presented in Appendix 3). Each individual plant was assigned six interference coefficient values - i.e. one value for its interference from all neighbouring¹² Leek plants, another for its interference from all neighbouring Beetroot, and so on with each species (including its own species). The proximity model was an additive reciprocal of distance model:

$$N_j = \sum_{j=1}^{j=12} (1 / d);$$

Interference coefficient (N_j) of focal individual to neighbouring individuals of species j = the sum (over all 12 individuals¹³ of species j in the same tank) of the reciprocals of distances of each from the focal individual. This distance model was felt likely to be advantageous because, firstly, it was the simplest so that any effects detected with it would be unlikely to be artefacts of an overcomplex model; and secondly, size of neighbours was not included because it would violate the assumption of the regression procedure that

¹² All Leek plants, that is, which are *deemed to be neighbouring according to the chosen distance model*: in this case all Leek plants in the same box as the focal plant.

¹³ But, effectively, 11 in the case of its own species since a plant's interface with itself was assigned a zero value.

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Figure 1. Box 1: Spatial locations occupied by plants.

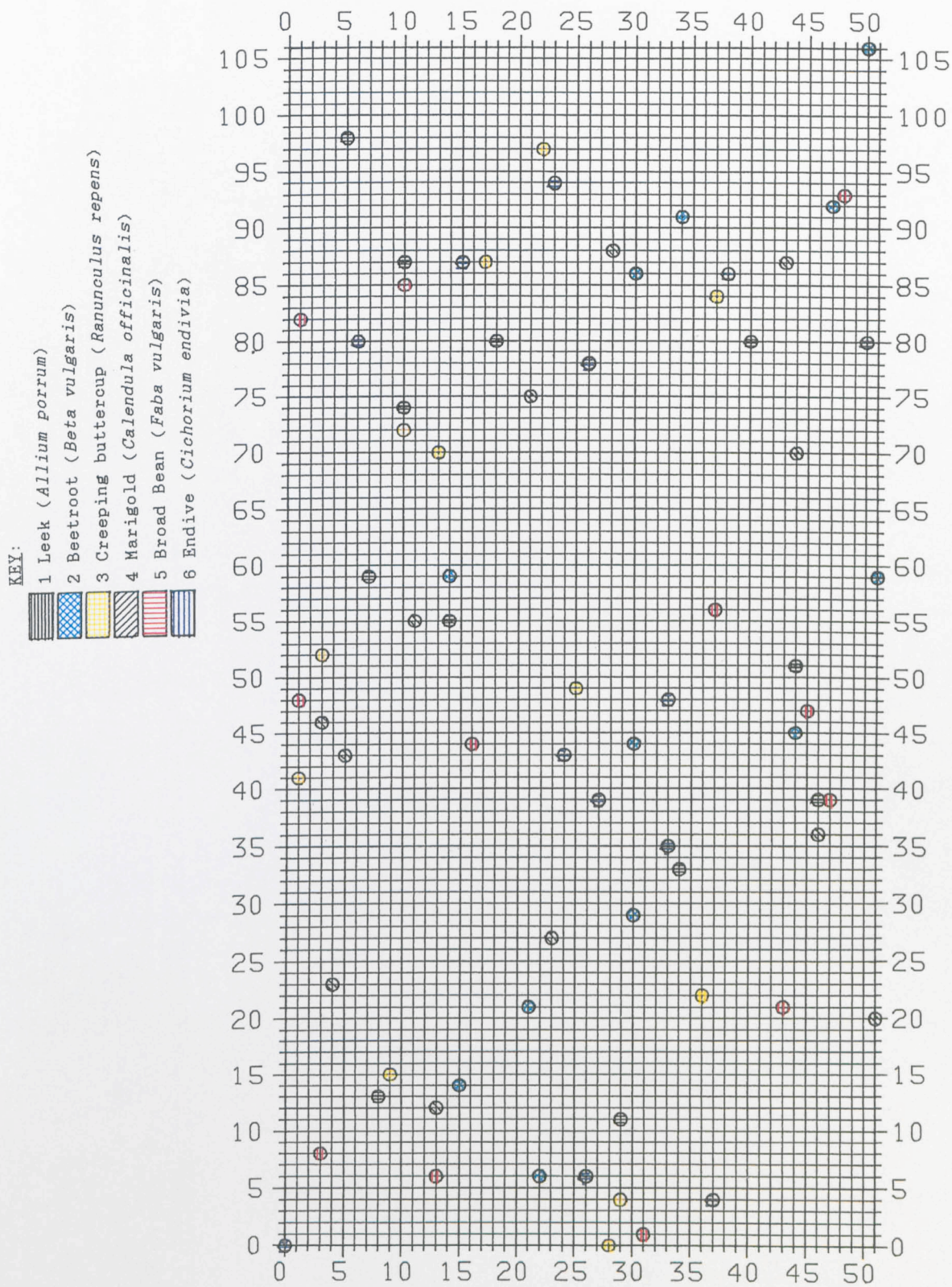


Figure 2. Box 1: Millimetre contour lines representing

height of the datum plane above the soil surface calculated and drawn using the UNIRAS UNIMAP package.

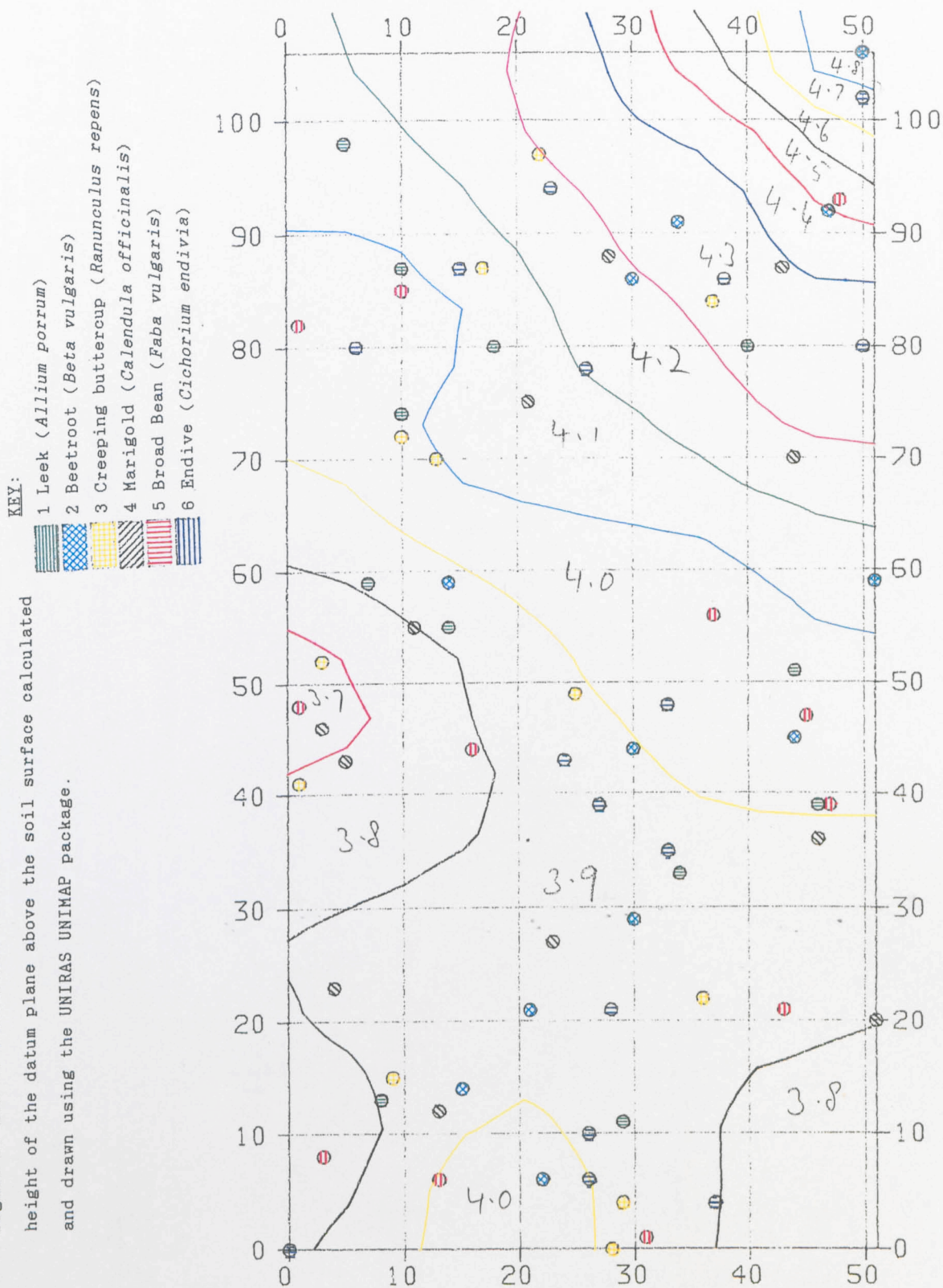


Figure 3. Box 2: Millimetre contour lines representing height of the datum plane above the soil surface calculated and drawn using the UNIRAS UNIMAP package.

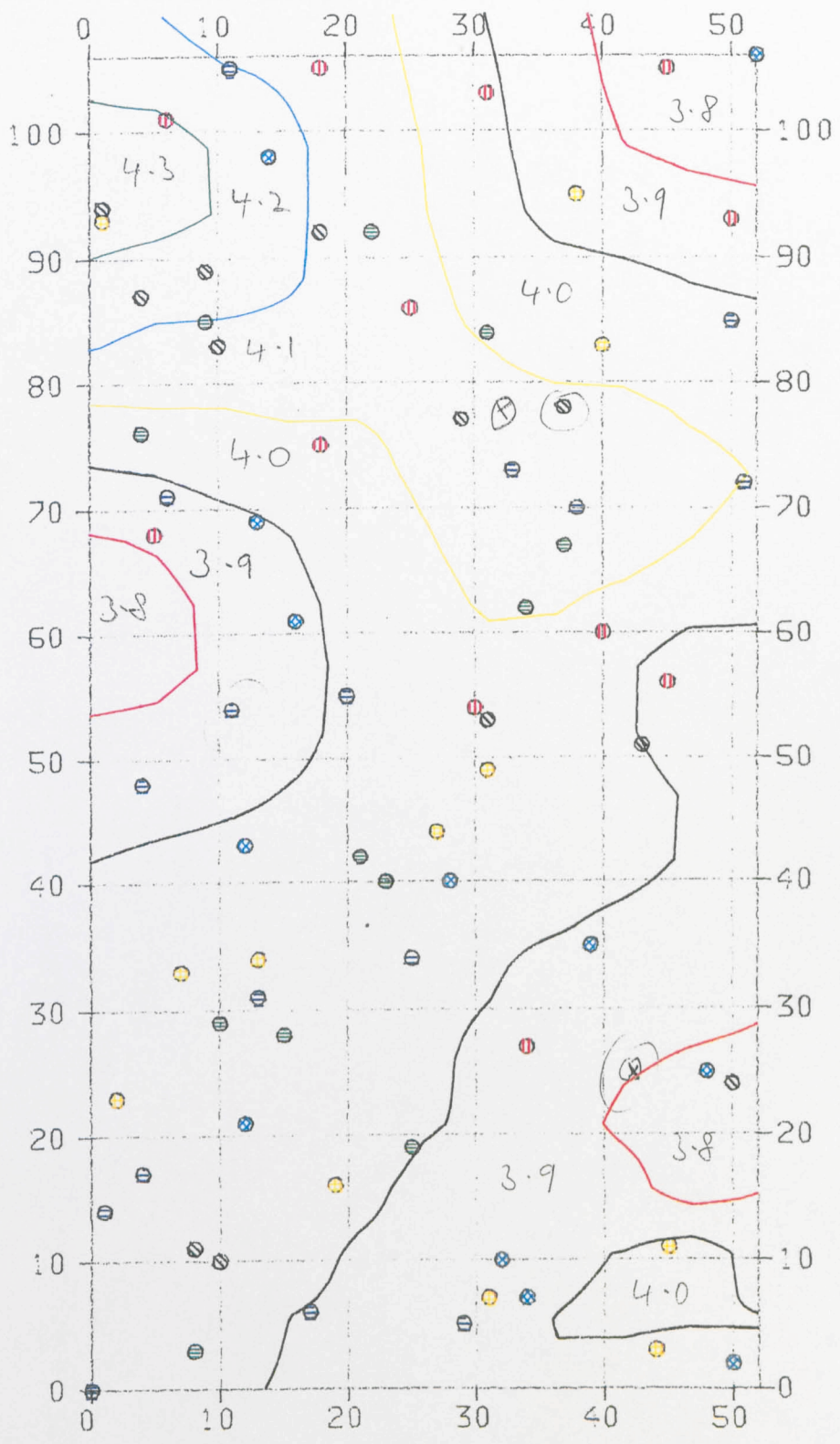
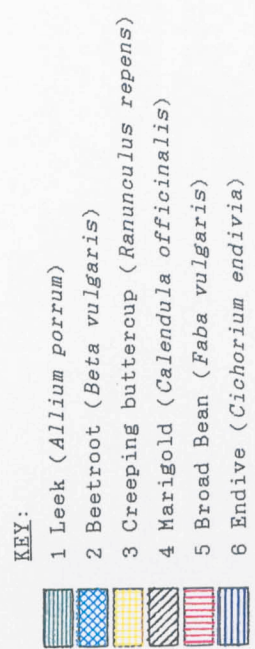
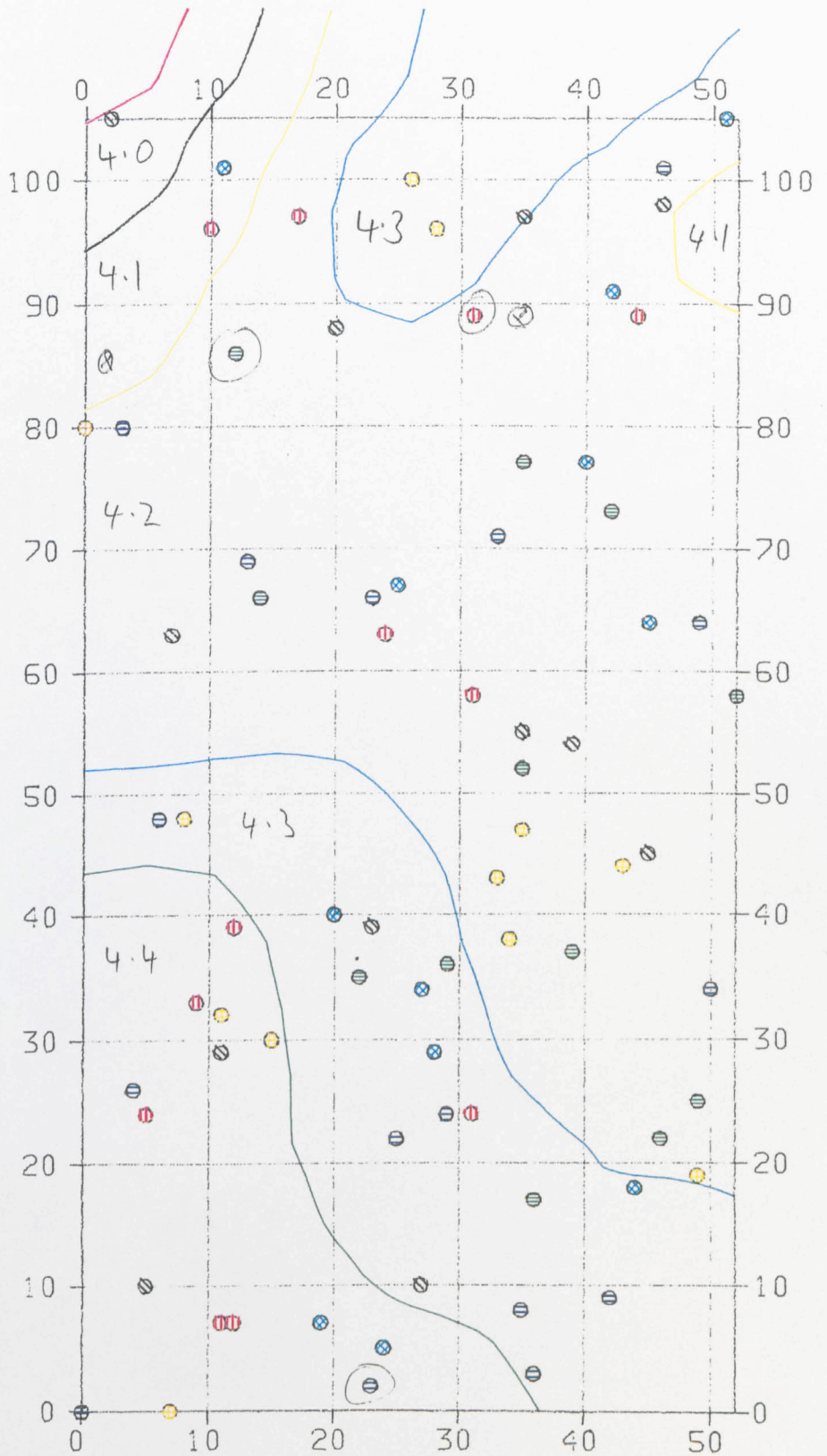
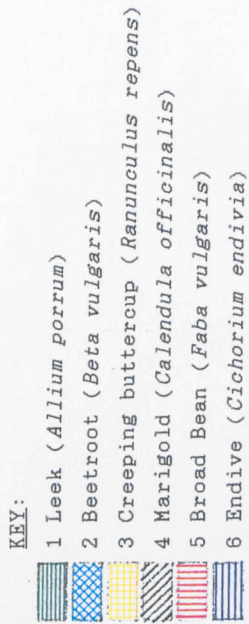


Figure 4. Box 3. Millimetre contour lines representing height of the datum plane above the soil surface calculated and drawn using the UNIRAS UNIMAP package.



8.3 Statistical analysis

Inspection of the data revealed a problem. The uniform random numbers used to produce planting positions generated interference coefficient distributions with a few extreme outliers resulting from those plants which happened to have a very close neighbour. Data for plants having any interference coefficient of 0.1 or greater were therefore excluded from analysis; the excluded data represents that part of the response curve in which the deleterious effects of competition from neighbours would be expected to be strongest.

Multiple regression analyses were carried out of the z-scores of heights and fresh weights on the six interference coefficient z-scores using backwards elimination of independent variables. Programs and data are presented in Appendix 3.

8.4 Results

Table 4 shows the statistically significant effects of interference coefficient z-scores on fresh weight z-scores at harvest; Table 5 significant effects on height growth rate (cm per day); Table 6 significant effects on shoot height (cm). The significance level in the last column of the tables represents a two-tailed student's *t* test of the null hypothesis that there is no linear relationship - i.e. that the regression coefficient deviates from zero due to sampling error.

Table 4: Effects of interference coefficients on fresh weight z-scores at harvest.
(36 days for Broad Bean; 67 days for other 5 species)

Focal species	Neighbour species	Regression coeff.	Sig. T
Broad Bean	Endive	1.601	0.0035
Leek	Beetroot	-2.147	0.0457
Marigold	Broad Bean	-4.162	0.0022

Table 5: Effects of interference coefficient z-scores on height growth z-scores.

Focal species	Day of msrmnt.	Neighbour species	Regression coeff.	T	Sig. T
Beetroot	7	Leek	5.54348	4.128	.0010
Beetroot	36	Leek	-5.17024	-3.512	.0031
Bean	28	Leek	1.59142	2.252	.0337
B'cup	21	Beetroot	2.41231	2.275	.0405
Marigold	21	Beetroot	1.73197	2.852	.0157
Leek	67	B'cup	2.96945	2.584	.0182
B'cup	36	B'cup	-1.44849	-3.810	.0029
Beetroot	7	Marigold	-2.73913	-3.534	.0033
Beetroot	36	Marigold	2.70318	3.287	.0050
B'cup	36	Marigold	5.14972	5.310	.0002
Marigold	7	Marigold	-2.07852	-3.915	.0024
Marigold	14	Marigold	3.34365	5.769	.0001
Marigold	21	Marigold	1.27786	2.290	.0428
Endive	21	Marigold	2.14508	4.303	.0005
Endive	67	Marigold	-1.45248	-2.820	.0129
Leek	36	Bean	-2.21200	-3.746	.0014
B'cup	43	Bean	-1.76446	-2.335	.0350
Marigold	7	Bean	-1.73708	-2.979	.0125
Marigold	28	Bean	-5.30471	-4.265	.0013
Marigold	50	Bean	3.31891	2.561	.0237
Bean	7	Bean	1.35511	2.643	.0137
Bean	28	Bean	-1.20881	-2.077	.0487
Endive	14	Bean	1.57852	2.255	.0406
Endive	36	Bean	-2.18876	-4.500	.0004
Leek	67	Endive	-1.33832	-2.230	.0380
B'cup	43	Endive	1.46765	2.604	.0208
Marigold	7	Endive	1.61412	4.065	.0019
Marigold	28	Endive	1.39992	2.873	.0152
Bean	21	Endive	1.32841	2.477	.0207
Endive	14	Endive	2.09828	2.332	.0351
Endive	67	Endive	1.75652	2.604	.0199

Table 6: Effects of interference coefficient z-scores on height z-scores.

Focal species	Day of msrmnt.	Neighbour species	Regression coeff.	T	Sig. T
Leek	21	Leek	1.96469	2.204	.0407
Leek	50	Leek	1.94203	2.186	.0423
Leek	67	Leek	2.03864	2.235	.0383
Beetroot	21	Leek	4.49586	2.634	.0188
Bean	28	Leek	1.31597	2.529	.0184
Endive	14	Beetroot	2.96182	2.863	.0119
Endive	21	Beetroot	2.46230	2.672	.0174
Endive	28	Beetroot	2.33607	2.272	.0372
Endive	36	Beetroot	2.71442	2.625	.0184
Endive	43	Beetroot	2.82765	2.854	.0115
Endive	67	Beetroot	2.33080	2.316	.0375
Endive	67	B'cup	1.40978	2.271	.0408
B'cup	43	Marigold	3.01405	2.437	.0268
B'cup	50	Marigold	3.00253	2.359	.0314
B'cup	67	Marigold	3.39991	2.342	.0316
Marigold	14	Marigold	2.74336	3.431	.0056
Marigold	21	Marigold	2.81953	3.596	.0042
Marigold	28	Marigold	3.11184	4.112	.0017
Marigold	36	Marigold	2.95797	3.658	.0038
Marigold	43	Marigold	1.82498	2.488	.0346
Marigold	50	Marigold	1.89978	2.287	.0480
Marigold	67	Marigold	1.77617	4.235	.0012
Endive	14	Marigold	1.48596	2.589	.0206
Endive	21	Marigold	1.46929	2.717	.0159
Endive	36	Marigold	1.30879	2.235	.0400
Endive	43	Marigold	1.44270	2.572	.0205
Leek	43	Bean	-1.63057	-2.246	.0368
Marigold	7	Bean	-2.74588	-3.682	.0028
Marigold	43	Bean	-4.11824	-3.211	.0106
Marigold	50	Bean	-3.67329	-2.529	.0323
Bean	7	Bean	1.35686	3.060	.0052
Bean	14	Bean	1.39381	3.343	.0027
Bean	21	Bean	1.17458	2.852	.0090
Endive	28	Bean	1.18770	2.162	.0461
Marigold	7	Endive	1.09681	2.402	.0320
Bean	7	Endive	1.49630	3.337	.0027
Bean	14	Endive	1.47055	3.418	.0023
Bean	21	Endive	1.78051	3.974	.0006
Bean	28	Endive	1.29638	2.932	.0073
Endive	67	Endive	1.50021	2.401	.0320

The significance levels tabulated should be interpreted in the light of the number of comparisons being drawn in each case (Ried and Hall, 1984) - viz 36 for Table 4 and 264 for Tables 5 and 6. The results may indicate that sample numbers should have been larger;

however it seems that some biological interactions have been shown up by the proximity analysis. The results of interest are not, of course, the significance levels themselves; but the relationships they refer to, represented by the regression coefficients. Several aspects of the results are noteworthy.

- a) There are 12 negative effects of proximity on height growth rate (of which 6 are due to Broad Bean - which, being the largest plant, would be expected to reduce the growth resources available to its neighbours the most); but there are also 19 positive effects.
- b) Apart from proximity to, again, Broad Bean - which has four negative effects on height of neighbours - *all* effects on height are positive throughout the period of measurements. This might be due to etiolation caused by shading.
- c) Few effects of or on Buttercup are seen in the results, and this is probably because the neighbourhood model employed, based on the location at which it was planted, is least realistic for this species due to its horizontal growth and habit of rooting at intervals in different places. The fact of Buttercup showing little effect may be taken as validating the reality of effects of other neighbours.
- d) More generally, the three largest species (Marigold, Broad Bean and Endive) have most effects on neighbours - which might be expected; yet they also experience the most effects *of* neighbours, which is hard to explain.
- e) There is some congruence between the fresh weight results and the others: Endive has a positive effect on Broad Bean's fresh weight as well as its height and growth rate. Similarly the strongly negative effect of Broad Bean on Marigold fresh weight parallels negative effects on the other two parameters.

The majority of relationships indicated by the analysis have positive regression coefficients. What this suggests is that proximity to other plants - particularly Marigold and Endive - increased plant height growth under the conditions of the experiment.

Three further sets of regression analyses were carried out for z-scores of fresh weight, height and height growth rate. In these analyses instead of treating each focal species separately all individuals were entered into the regression together (focal species being represented by five dummy variables up to day 28 and four thereafter). The capability to thus deal with unlike variables together is a useful property of z-scores. There were no generalized effects of interference coefficients on fresh weight; Tables 7 and 8 show generalized effects on height and height growth rate. Here there are 48 comparisons being drawn.

Table 7: Effects of interference coefficient z-scores on height z-scores of all species present.

(six species up to day 28, five species subsequently)

Day of msrmnt.	Neighbour species	Regression coeff.	T	Sig. T
67	B'cup	.53064	2.016	.0468
14	Marigold	.30348	2.506	.0136
21	Marigold	.36325	3.309	.0013
28	Marigold	.32449	3.133	.0022
36	Marigold	.98518	2.785	.0066
43	Marigold	.89608	2.570	.0119
7	Bean	.23895	2.248	.0263
14	Bean	.30955	2.829	.0055
21	Bean	.27178	2.719	.0076
28	Bean	.19622	2.117	.0365

Table 8: Effects of interference coefficient z-scores on height growth rate z-scores of all species present.

(six species up to day 28, five species subsequently)

Day of msrmnt.	Neighbour species	Regression coeff.	T	Sig. T
14	Leek	.33995	2.254	.0262
14	Marigold	.41800	2.482	.0146
21	Marigold	.38279	2.229	.0278
36	Marigold	.63298	2.109	.0378
7	Bean	.34790	2.712	.0078
14	Bean	.34402	2.230	.0277
36	Bean	-1.24902	-3.904	.0002
43	Bean	-.88330	-2.042	.0443
7	Endive	.31671	2.561	.0118

Some dummy variables representing focal species were significant, indicating that there were statistically significant differences between species in the way they react to the proximity of neighbours. Even so, the pattern of results shows similarity with the results for effects on individual species, confirming the existence of real positive effects on height and height growth. Interference from Marigold again yielded the most positive regression coefficients and Broad Bean again differed from the other species in producing some negative effects.

Chapter 9. Discussion

The reported experiment vindicates neighbourhood distance modelling as a workable method for determining how neighbouring plants affect an individual in a multispecies cropping situation. This despite the extreme simplicity of the models used for interference (sum of reciprocal distances) and regression (straight line not forced through the origin).

There is considerable scope for the further improvement of neighbourhood distance modelling by the building of more complex interference models which more nearly reflect the mechanisms of inter-plant interactions (Benjamin and Sutherland, 1992; Mou *et al.*, 1995).

Since actual interactions between plant neighbours may occur separately with respect to each different resource, there may be a need to include interference for each resource as a separate sub-model: Z-scores for one interference coefficient reflecting our beliefs about how plants interfere with each others' supply of phosphate; another for potassium; another for nitrogen, a fourth for light, and so on. Z-scores could then offer a simple means of entering such sub-models into a single multiple regression equation. Another use of z-scores could be to allow use of different sub-models for, say, light interference from different species in the same experiment.

One factor which must act as a brake on the evolution of better distance models is the considerable time and trouble needed to produce experimental data for fitting models to. This could be alleviated if workers in the field were to make their raw data available freely on an internet site for use by others. The problem with such an idea is likely to be unwillingness of workers to publicize their data for various reasons. This could be countered by an inducement: The site undertakes that all users will have to pass through a copyright screen that prompts them to assent to a set of conditions before entry to the site. These might include an undertaking to cite the worker who supplied any data which subsequently gives rise to any publication in that publication (for example citation of all papers published by the supplier based on said data, or, if none exist, a citation in the acknowledgements section); and undertaking to send a copy of any publication arising within a month of receiving acknowledgement from the publisher.

9.1 Further uses of distance models

An advantage of distance models over other methods which have been developed to study the effect on yields of growing crop plants in species mixtures, is that it offers the potential to draw the *whole curve* of yield as a function of spatial relationships with neighbours instead of only (usually) three points on it (two sole crops and one mixture of

them). This should be capable of development to a method enabling specification of optimal mixtures. It may be especially useful at detecting and quantifying three-way, or higher, interactions between species (i.e. a statistical interaction between proximities to two species).

The method could be used to detect and quantify effects of annual plants on the tree components of agroforests. In doing this it might be simpler if the annual plants, instead of being positioned individually, were positioned in blocks of suitable size and distribution, and measures of the blocks, rather than of individual plants within them, were used. The ideal planting pattern is probably not fully random, but chosen to give a wide and even distribution of interference coefficient values, without extreme outliers. This will depend, of course, on the choice of interference model.

9.2 Optimization of multispecies planting patterns

The analysis method which I have described thus far has two stages. The first is to specify a model describing the expected degree to which one plant affects another and use it to assign interference coefficients to individual plants¹⁴ in an irregular planted pattern. The second is to regress any individual responses of interest on the interference coefficients to obtain a regression equation whose signed coefficients represent the degree to which each type of plant present affects each.

How might we proceed from this to a method for optimising planting patterns? First would be needed a catalogue of known neighbour effects for pairs of species/cultivars. This data would have to be built up from field experiments using neighbourhood distance modelling, although it might be possible to use results of conventional mixture trials (two sole crops plus one mixture) as a crude substitute, where necessary. The catalogued data would also need to be classified according to the environmental conditions under which plants had been grown. Such a catalogue would probably actually need to contain data which were comparable (either in the sense that the same few distance models were consistently used for all; or in that the raw data were catalogued, leaving it to the would-be optimiser to derive his or her own fitted lines or curves). However I will here make the simplifying assumption that a catalogue has been assembled using a single definition for interference coefficients (say sum of $1/d^2$); and containing, for each species or cultivar pair, an equation relating yield of focal species to interference coefficient of the neighbour

¹⁴ Perhaps the method might be stated a little more widely: blocks of plants could be treated as well as individuals, and interference coefficients could be assigned for other aspects of the environment than neighbouring plants.

species. Thus one equation for coffee yield against rubber tree interference, another for rubber tree yield against coffee interference, and so on.

Suppose, now, that an optimal design is required for a cacao+banana agroforest and, to simplify the example, that there will be no requirement for the passage of machines between the plants. The core of the optimisation program is an algorithm which is given, as input data, the planting pattern of a unit cell of the agroforest, and produces, as its output, The yields of each component species per unit area. It does this by applying the catalogued equations for the species pairs in the cell, and applying them to each plant in the cell as a focal plant. In calculating interference coefficients, however, it sums interference not only from neighbours in the cell, but from also those in neighbouring, identical cells. It would be preferable to express these results as LERs, which requires sole crop yields for both species. This could easily be obtained by running the core algorithm against input data representing sole crop unit cells.

Given this capacity to evaluate the expected production of any specified unit cell either of two methods could be used to produce an optimal unit cell: linear programming or a genetic algorithm. I will deal with the latter. Geake (1993) describes a genetic algorithm which was used to produce an optimal timetable for university examinations. The timetabling program first produces 100 random timetables, dividing them into 50 pairs which mate with each other. A simple code represents the exam timetable. For example, 3,7,11,2,7 represents the timetable in which exam 1 occupies the third time slot, exam 2 the seventh. Every pair produces two "offspring" which take their characteristics from their parents. When the parent 3,7,11,2,7 is mated with another parent, such as 1,2,3,4,5, the digits or "genes" are swapped about, for example by swapping the first three and the last two to give 1,2,3,2,7 and 3,7,11,4,5. Each second-generation timetable is then scored on how well it fits the timetabling conditions. The program next mates 50 pairs from the second generation. The probability of a particular timetable being chosen depends on its score, so the best could be selected several times. A very good timetable may mate with itself - in which case its offspring would be identical to it. The program is run for many iterations, producing better and better timetables by what is, in a very precise sense, a process of evolution.

Such a procedure could be directly applied to the agroforest optimisation problem if the agroforest unit cell can be represented by a string of numbers. This is a problem, but a soluble one. For example the agroforest unit cell could be divided by a grid into a number of squares, say 100; and then represented by a string consisting of three values for each square: x- and y- coordinates and a number representing the species/cultivar planted in the

square (a zero representing that there is no plant in that square). Probably it would be necessary to design the mating subroutine to have a high probability of producing offspring unit cells with about the same number of plants as the parents.

Since a genetic algorithm requires computational resource in proportion to the number of calculations in each iterative step and to the data storage space required by each string, there is a trade-off between the cost of computing and precision of the result. The more finely the grid squares divide up the unit cell, the more computer memory will be needed to store it and the more computation will be needed per mating. The more complex the equation relating cacao yield to banana interference, the longer it will take to score each unit cell. We therefore would do better with a more structured string representation of the unit cell which did not need to take up a lot of space with zeros. However, I am concerned here to indicate the broad approach rather than to go into fine details of the program's design.

In sum, some unit cells of an agroforest would be set up at random in a computer. The genetic algorithm mutates the planting patterns by breeding from them; the productivity (or whatever is of interest) of the cells in each generation is calculated based on regression equations derived from experiments such as that described above; and the more productive unit cells are selected iteratively. Constraints such as minimum gaps for passage of agricultural implements could be incorporated into the set of rules within which mutation is allowed to operate.

There remain problems to be solved. Uniform-randomized plant locations can result in interference coefficient values which bunch too narrowly, yet also have extreme outliers. An alternative method of generating plant locations therefore needs to be developed which can give a better spread of values. The difficulty here will be that of avoiding any systematic bias. One avenue could be to enlarge the rule that a random point coordinate is discarded if it coincides with one already drawn, to discard, additionally, point coordinates too close to any already drawn. My results appear to suggest that in the case of a six-species mixture, 36 data points for each species is, at least, enough to be useful.

Z-scores supply a useable means of aggregating unlike variables in regression equations used for distance models, whether the variables are unlike in respect to species or whether they represent unlike sub-models constituting a neighbour interference model. This allows the modelling of a multispecies situation.

Based on neighbour interference modelling, it would appear possible to develop an optimisation procedure for mixed crop designs using a genetic algorithm approach. The

output from this would be a design predicted to be a productive one, with yields expressed as LER values.

PART III. ON THE POSSIBILITY AND POSSIBLE MECHANISMS OF
INTER-SPECIFIC COOPERATION BETWEEN COMPETING,
NEIGHBOURING PLANTS.

Chapter 10. Summary of Part III

According to Newman (1988) 'It is generally assumed that when interactions between plants involving nutrients occur they are competitive'. Using concepts of Evolutionary Game Theory, this study examines the question of cooperation in plants: both between the green plant and its associated vesicular-arbuscular mycorrhizal (VAM) fungi; and between neighbouring green plants connected by common VAM fungal hyphae. Its main thrust is to ask not '*do* plants cooperate?'; but 'if plants cooperate, *how* might they do so?'

Exploring the implications for this debate of Axelrod and Hamilton's (1981) game theoretical approach to the evolution of cooperative behaviour (not previously applied to plant behaviour, so far as I am aware), it attempts:

- a) To point out that that there is a serious and unexamined logical problem in the conventional view that the relationship between a green plant and an associated VAM fungus is mutually beneficial. That the association is of mutual benefit would be insufficient to explain its persistence, and the fact that it *does* persist should tell us something about its structure.
- b) To show that there is no logical paradox in postulating the *simultaneous* existence of competition for resources *and* of resource-sharing cooperation between a given pair of neighbouring green plants.
- c) To show that resource-sharing cooperation is likely to confer added fitness on some plants - particularly stress-tolerant strategists (*sensu* Grime, 1973)
- d) To show that at least a certain minimal type of cooperation may be deemed to exist between VA mycorrhizally-connected green plant neighbours.

Some evidence in the literature is indicated that further development of cooperation in plant communities (beyond the 'minimal type' of cooperation) has occurred; and is difficult to explain in any other way. Possible evolutionary stages through which this could have happened are discussed.

The *assumption* that plants do not cooperate is no longer safe and should now be considered a hypothesis for which evidence is wanting. Two experiments are described which failed to show that plants do indeed cooperate; but whose designs may be considered worthwhile as prototypes for future attempts at investigating inter-plant cooperation.

Scientific implications of the possible existence of inter-plant cooperation for Plant Ecology and possible economic implications for Agroforestry and mixed timber plantings are indicated. A rich field is open for further research and suggestions are made for directions and methods to be adopted.

Chapter 11. Introduction

The debate on resource transfers between neighbouring plants mediated by mycorrhizal fungi has so far concentrated on the question 'does net transfer occur?'. Having argued that the evidence that it does is strong, this work then takes a different approach: looking at the logic which would have to underlie such inter-species cooperation. The elegantly simple evolutionary game theoretic approach of Axelrod and Hamilton (1981), which contributed to scientific understanding of the nature of cooperation and of the conditions necessary for it to evolve is described. This theory is first applied to the case of the simple relationship of a mycorrhizal fungus with one green plant, conclusions being drawn about the type of control which the plant partner must be able to exert over the fungus in order for the mutualism of the symbiosis to remain evolutionarily stable.

These conclusions are applied to the case of a single mycorrhizal fungus simultaneously linked to two different plants, and a further conclusion drawn that this system constitutes at least a certain minimal type of cooperation - 'interface-based' cooperation - between the two plant partners.

Evidence is indicated that some further evolution of cooperation may have taken place among green plants, on grounds of their observed abilities. A pathway is suggested of stages which this further evolution may have taken, and an experimentally simple test of the hypothesis presented.

Although there are many similarities between VAM and ectomycorrhizal (ECM) associations, there are also important differences. I deal here with VAM associations.

11.1. Evolutionary game theory

Before describing game theory of the evolution of cooperation between unrelated organisms, I need to present some of the basic concepts and terminology of evolutionary game theory. Riechert and Hammerstein (1983) describe the game theoretic approach to evolution: 'Game theory is the study of conflicts of interest in which the value of a particular set of actions undertaken by a "decision-maker" depends not only on his own choices but also on those of others. [...] The decision makers are termed players and the objective function of optimization theory is called the payoff function. This function assigns a value or measure of success to the benefits received from playing a particular strategy, which specifies how a player will act in all potential situations. The game, then, is a collection of rules known to all players that determines what each player can possibly do and the outcome of using particular choices or strategies.'

'[...] In classical game theory, a player's payoff is measured subjectively and is defined by personal value judgements of what constitutes success. In contrast, a neo-Darwinian analysis of this type of contest replaces the subjective notion of success with an objective criterion. The players payoff is measured as the change in expected Darwinian fitness resulting from playing a particular strategy. [...] In most classical applications, game theory focuses on decisions made by humans using cognitive choice. The evolutionary application of this construct focuses on decisions "made by" the process of natural selection - individual plants and animals are merely the performers of an inherited program.'

Chapter 12. Game theory of the evolution of cooperation

Axelrod and Hamilton (1981) used a game theoretic approach to investigate the evolution of cooperation. They state the problem succinctly:

'Many of the benefits sought by living things are disproportionately available to cooperating groups. [...] The problem is that while an individual can benefit from mutual cooperation, each one can also do even better by exploiting the cooperative efforts of others¹⁵. Over a period of time, the same individuals may interact again, allowing for complex patterns of strategic interactions'.

They used the Prisoner's Dilemma game for their analysis. In the Prisoner's Dilemma game, it is open to the two players to defect against or cooperate with each other. Whatever the other player does, defection yields a higher payoff than cooperation. However if both defect, both do worse than if both had cooperated.

Figure 5: Illustrative payoff matrix for the Prisoner's Dilemma Game. (from Axelrod and Hamilton 1981)

		<u>Player B</u>	
		C Cooperation	D Defection
<u>Player A</u>	C Cooperation	R=3 Reward for mutual cooperation	S=0 Sucker's payoff
	D Defection	T=5 Temptation to defect	P=1 Punishment for mutual defection

Thus the game is defined by a 'payoff matrix' (such as that in Figure 5) in which

$$T > R > P > S \text{ and}$$

$$R > (S + T)/2$$

They state that defection is the solution, in evolution as in game theory, to the one-throw version of the game. I.e. evolution will favour defectors if the interactions between pairs of individuals are random and not repeated.

¹⁵ There is another type of cooperation in which no (short term) cost is associated with a decision to cooperate. The herbivore which allows its hide to be cleaned of parasites by a bird, for example, might incur no such cost. In this study, I am concerned only with situations where cooperation *has* a short term cost.

However if the Prisoner's Dilemma (PD) game is *repeated* between the same two players, cooperation can become the rational solution. Axelrod set up a tournament version of the game on a computer, in which after the current interaction there is a probability w that the same two individuals will meet again. Game theorists in various disciplines submitted strategies to the tournament, some using complex mathematical analyses of the past behaviour of a partner to determine their play. The winning strategy, named 'Tit for Tat', was also the simplest. Its specification consisted of the rule: 'cooperate on first meeting, and thereafter do whatever the other player did in the previous move'. Axelrod showed that, provided w is large enough, Tit for Tat strategy is robust and stable.

For cooperation to be able to invade a world of defectors, the authors point out that there must be an initial cluster of neighbouring cooperators. This might evolve initially through true altruism between close kin; but once a cluster of cooperators is so established it becomes possible for unrelated individuals to cooperate with individuals belonging to it.

In summary, the requirements which must be satisfied for PD cooperation to be evolutionarily possible are that

- a) there must be a reward for mutual cooperation;
- b) probability of re-encounter must be sufficient;
- c) an individual 'must not be able to get away with defecting without the other individuals being able to retaliate effectively.'

Axelrod and Hamilton say of this that the defecting individual must not be lost in 'an anonymous sea of others'. Higher organisms avoid this problem by an ability to recognize many different individuals, but lower organisms 'must rely on mechanisms that drastically limit the number of different individuals or colonies with which they can interact. [...] When an organism is not able to recognize the individual with which it had a prior interaction, a substitute mechanism is to make sure that all of one's interactions are with the same interactant. This can be done by maintaining continuous contact with the other. This method is applied in most interspecies mutualism, [for example] a tree and its mycorrhizal fungi¹⁶.' According to Dawkins (1989, p202): "Reciprocal altruism [...] is at work in all relationships that are symbiotic."

¹⁶ I will argue below that, while the mycorrhizal symbiosis may have originally arisen through this method, there is evidence that it has since evolved further as its present day character would not appear to be able to restrain defection by the fungus in this way.

Chapter 13. Evolution of cooperation in plant communities

In trying to understand the structure of cooperative relationships in plant communities I will first look at the 1:1 association between a single VAM fungus and its host plant, which is generally accepted as being a case of cooperation. Then I will move on to look at the more complex case of the 1:1:1 situation in which two plants are linked by a single VAM fungus having interfaces with both. In doing so I will need to use two viewpoints: how can a strategy *arise* through evolution, and how can it *remain* evolutionarily stable - that is, avoid being supplanted by the successful invasion (or locally arising mutation) of another strategy.

13.1. 1:1 Cooperation between a VAM fungus and plant

In this section I will argue that:

- a) Some mechanism *maintains* the mutualism of the association, preventing its decline into parasitism by the fungus.
- b) This mechanism is unlikely to be merely that those plants associating with more beneficial (as against more parasitic) fungal strains survive better, thus causing improved survival in their symbionts.
- c) Somehow, therefore, green plants must be able to *selectively* involve themselves in associations with those strains of VAM fungi which are most beneficial to them.

It is widely accepted that, although there may be exceptions, *the relationship between a plant and its mycorrhizal fungus is, generally, one of mutualistic symbiosis*. That is to say the relationship is profitable to both parties in the sense that it increases the (Hamiltonian) fitness of each. Abundant evidence indicates that the profit to both parties consists in the fact that the association enables each to *trade resources* with the other (Tinker, 1980). From this trading, the VAM fungus obtains assimilated carbon (which it is probably unable to obtain from any other source but a plant host¹⁷), whilst the plant obtains an improved supply of mineral nutrients of which phosphorus is especially important¹⁸, although nitrogen, potassium and others can also be involved.

However, the fact of being mutually beneficial is not a sufficient condition for the symbiotic relationship to come into being; or, once evolved, for it to survive since it is now generally accepted that natural selection operates at the level of the individual rather than

¹⁷ There is no evidence that VAM fungi have any saprophytic ability (Smith and Gianinazzi-Pearson 1988).

¹⁸ However, Read (1991) challenges the view that the main function of a mycorrhiza for the plant is to aid phosphorus nutrition, arguing that there is evidence of a diversity of types of mycorrhizal association to suit different biomes.

the species (Grafen 1984). Consider this situation: a symbiotic relationship has somehow arisen between populations of VA mycorrhizal fungi and plants such that the fungi infect plants and then pass mineral nutrients to them; while the plants supply the fungi with assimilated carbon. What is to stop the fungus defecting? If a mutant strain of VA mycorrhizal fungus arises which uses a higher proportion of the resources available to it for its own growth and reproduction, thus passing less resources to the plant, what is to prevent it being more successful than the original genotype? Clearly some mechanism *does* prevent this happening. If not, then such a (relatively) parasitic mutant strain would supplant strains which are beneficial to plants, yet it seems clear that beneficial fungal strains do in fact persist¹⁹.

13.2. What mechanism selects in favour of more beneficial fungal strains?

Three possible means suggest themselves whereby the decay of mycorrhizal symbioses into parasitism could be prevented:

- a) the 'selfish' VAM strain is so dependent on the individual host plant that any action which lowers the fitness of the host would thereby immediately harm the fitness of the fungus; or else
- b) an ability of the plant partner to 'retaliate' against defection by cutting off the flow of resources to a defector, or
- c) to the defector's offspring²⁰.

What, however, if the answer to this question is that the fungus is subject to such strong and detailed physiological control by the plant that it has not sufficient autonomy to be *able to defect*²¹? I am not going to entertain this possibility further (even though I do not think that it can be discounted²²), because it would not constitute a *solution* to the conundrum; merely a way of displacing it back into the evolutionary past. As such it does not materially affect my argument.

13.2.1. Selection via effect on plant fitness

It could be thought that the 'selfish' mutant fungus, although initially more successful, might eventually lose fitness because the lowered fitness of its host plant results in restriction of the supply of carbon assimilate. However this seems unlikely to be the case. In the first place most parasites do, in fact, lower their host's fitness without appearing to

¹⁹ The ubiquity of the association is perhaps the most compelling evidence of this.

²⁰ Or close relatives.

²¹ If this is the case then we have a situation very similar to that of the organelle which originated as a separate organism.

²² But see below.

cause problems for themselves in the process. Secondly, it appears that the plant invests resources in the association (until several weeks after germination of the fungus according to Smith and Gianinazzi-Pearson, 1988) before it begins to gain from it in terms of growth²³. Plant root systems interpenetrate in most habitats, and VAM fungi are promiscuously able to infect most species and can travel fast through soil (rates up to 2.5 cm per day are reported by Scheltema *et al.* 1987). The 'selfish' mutant should therefore have ample opportunities to infect new plants and it is implausible that even the death of the original host would seriously impede it. It is also the case that more than one VAM fungus individual is usually associated with a plant, so that the defection of a single individual would be unlikely to have much effect on plant fitness.

13.2.2. Selection via plant 'retaliation' against an *individual* defector

Axelrod and Hamilton (1981) briefly mention the case of cooperation between a plant and mycorrhizal fungus. The plant must be able to retaliate against a defecting mycorrhizal fungus, by itself defecting (i.e. ceasing to supply carbon assimilate). But they surmise that it does not need an ability to *recognize* the fungal strain, because continuous contact is maintained. The plant would, nevertheless, require an ability to monitor resource flows both inwards and outwards through its interface with the fungus; on the basis of this monitoring to evaluate the utility of the fungal symbiont concerned; and to cut resource flows to it.

This mechanism, although more plausible than the first, suffers some of the same defects: it does not square easily with the fact that, initially, the plant invests in the fungus more than it is being paid back²⁴. There would appear to be a time-window during which defection is possible. Furthermore the plant seems to behave in such a way that it would lose quite substantially if a fungus were to defect, leading to the suspicion that it must indeed have some effective means of retaliation which ensures that this is not likely to happen.

Having said that, it might well be a possible mechanism for the ancestral evolution of the association. The plant would have been unable to invest much resource before requiring a payback from the fungus (thus reducing T, the 'temptation to defect'), which would slow the rate at which the fungus could grow; and longer-lived roots would be better able to

²³ This might be expected since the fungal structures must require resources to grow before they can begin to function.

²⁴ To such an extent that, according to Smith and Gianinazzi-Pearson (1988), 'mycorrhizal plants appear less efficient [than non-mycorrhizal plants] during the early stages of growth and development of infection but more efficient at later stages.'

retaliate (because w would be higher). The benefit which the plant could have reaped from the association would thus have been small, but so would the possibility of defection by the fungus.

13.2.3. Selection *via* plant 'retaliation' against a defector's offspring

This mechanism would require that the plant be able to recognize the offspring or close relatives of a mycorrhizal fungus with which it has been associated in the past. If a plant already able to retaliate against an individual defector as described above (and thereby maintaining a beneficial mycorrhizal association) then evolved a capability to recognize VAM strains previously encountered, the effect on its fitness might be considerable. It would gain informationally. Previously each new infection point (of which there are very many in a typical root system) would have marked the start of a new relationship with a player of whose history nothing was known. The new ability to recognize would allow the plant to use its previous experience of a strain of fungus in deciding how to play against it: whether to allow it to infect at all, and then how much resource to 'entrust' to it. This would be a significant gain because of the way a single VAM fungus is able to proliferate and give rise to many new infection points. Relatively large initial investment of assimilate could be made before any significant payback of mineral nutrients, because the plant would now have the capacity to retaliate against defection.

There is evidence that the degree of infection by VAM fungi is under the control of the plant rather than the fungus (Buwalda *et al.* 1984)²⁵, but are plants able to recognize fungal strains - i.e. respond differently to different strains? Certainly the mycorrhizal symbiosis involves a complex set of recognition events around the time of infection (Anderson, 1988). It is not known how far VAM fungus' functions are under the control of plant genes, but infection events, at least, are likely to be so (Smith and Gianinazzi-Pearson, 1988).

My theory requires that there should be *facultative* specificity of plants to mycorrhizal fungus strains, yet the current view is 'that infection specificity is almost completely lacking in VAM associations' (Chanway *et al.* 1991). However, most of the small amount of work in this field has searched for *obligate* specificity - by presenting plants in different experimental treatments with different single strains of mycorrhizal fungus. Gliddon and Trathan (1985) quote A. Berrington (pers. com.) as having found that mycorrhizal associations with *T. repens* can be site/genotype specific; and McGonigle and Fitter (1990), working in a hay meadow, found that *Glomus tenue* (Greenall) I.R. Hall mainly infected *Holcus lanatus* L., while other "coarse endophytes", which could be physically

²⁵ And the findings of Louis and Lim (1987) may confirm this for a tropical rainforest soil.

distinguished from *G. tenue* were the main colonizers of *Ranunculus acris* L., *Plantago lanceolata* L. and *Phleum pratense* L. Chanway *et al.* (1991) suggest that a reassessment may be required of the view that VA mycorrhizal associations are non-specific.

Clearly much more work is needed in this important field. Experimental tests in the laboratory of facultative specificity must reflect the reality existing in the field. This will involve presenting spores of different VAM strains (including, perhaps, some which had been found infecting the plant in the field) simultaneously to a plants' roots, to determine if plants exhibit preferences for particular strains when choice is possible.

With the recent great improvements in techniques for characterizing the genome, this should present much less of a problem than it would have done when we had only morphological characters to work with.

13.3. 1:1 fungus-plant cooperation: a conclusion

I have taken this argument further than is required for my present purpose. The crucial point to be accepted is that, whatever may be the mechanism by which it does so (i.e. either through the ability to retaliate against an individual VAM fungus' only through their mutual interface; or through refusal of future infection by its offspring; or both), *the plant host acts to favour the survival and reproduction of fungal strains which are more beneficial to it.* This conclusion has implications for interactions between neighbouring green plants (see below); as, also, does the following:

To thus *select* fungal strains the plant must have some capacity:

- a) to record information about the behaviour of the fungus,
- b) to use this information in some process of 'making' decisions about how to behave toward the fungus (i.e. to cooperate or defect), and
- c) to execute these decisions.

13.4. Possible mechanisms

As regards the execution of decisions, the physiology of the arbuscule, which forms the interface between plant and VAM fungus, is interesting. Smith and Gianinazzi-Pearson (1988) describe as peculiar to VA mycorrhizae 'the formation of an intracellular interface in which wall material is reduced to a minimum and membrane-bound enzyme systems exist in both symbionts, capable of generating the necessary energy gradients for active transport. Such extreme specialization is absent in other haustorial host-parasite interactions where nutrient transport is unidirectional towards the parasite'.

Thus both symbionts appear to have the necessary machinery to control resource outflows to each other against concentration gradients.

Chapter 14. Direct resource transfers between green plants: a case of cooperation?

Thus far I have dealt with the 1:1 plant-fungus *system*, seeing it as primarily a resource-trading partnership. I now move on to consider the 1:1:1 case of a VAM fungus linking two plants to each other. How can the evolutionary game theory of cooperation be applied to a 1:1:1 system?

14.1. Hyphal links between neighbouring plants

Individual mycorrhizal fungal hyphae can be connected simultaneously to two plants of different species, forming a link between them. Such linkages have been observed directly between several pairs of different plant species both for ECMs (Read *et al.*, 1985) and for VAMs (Heap and Newman, 1980; Read *et al.*, 1985; Chiarello *et al.*, 1982). Read *et al.* (1985) observed linking VAM hyphae which were thicker and less branched than normal, (i.e. non-linking) hyphae, inferring that these may be adapted to transport nutrients between the two green plants. They termed them 'arterial hyphae'. Knowledge that such links form gave rise to the question of whether they may mediate 'direct' resource transfers between the two plants concerned. Newman *et al.* (1994) also observed VAM hyphae linking neighbouring plants.

14.2. Evidence on 'direct' resource transfers between green plants

Most investigations have concentrated on carbon or phosphorus transfers through VA mycorrhizal hyphae. The usual method has been to pass isotopically labelled nutrient into a ('donor') plant and then measure the isotope in a neighbouring ('receiver') plant²⁶ (e.g. Read *et al.* 1985, Finlay and Read 1986, Grime *et al.* 1987). When in the laboratory, an experimental contrast can be drawn between sterile and mycorrhizal growth media. These experiments have demonstrated transfer of the isotope to the receiver plant to be generally much higher in the mycorrhizal treatments. Sometimes plants unable to form VAM associations have been included in the container as a control, and negligible amounts of isotope are found in these.

Newman (1988) and Bergelson and Crawley (1988) argue that experimentation to date is inadequate because only transfer of molecules in one direction (from 'donor' to 'receiver') has been unequivocally shown. It is therefore possible that transfer is occurring in both directions at the same rate. *Net* transfer will not be demonstrated unless transfer in the

²⁶ The terms donor and receiver do not imply any particular ecological role for a plant so designated, merely whether or no the plant has been selected by the experimenter to be fed a labelled nutrient.

reverse direction (from the 'receiver' to the 'donor' plant) is also measured and found to be less, a shortcoming which Grime *et al.* (1988) recognised. It is important to note, however, that Read *et al.* (1985) reported a thirty-fold increase in carbon transfer resulting from a shading treatment of the recipient plants. Neither Bergelson and Crawley (1988) nor Newman (1988) address the problem which this result poses for their argument that net transfer may not occur.

In illustration of this argument, Newman employs the analogy of two compartments containing solutions of H_2PO_4^- at equal concentrations, separated by a permeable membrane. In such a system, he points out, carrier-free $\text{H}_2^{32}\text{PO}_4^-$ starting in one compartment will soon be present in the other, but without any net transfer of phosphorus having occurred. Although Newman's use of this analogy is only illustrative, he does not postulate any *other* mechanism which could give rise to zero net transfers, and it needs to be pointed out that such a system would give rise to zero net transfers *only so long as concentrations in the two compartments remained equal*. If concentrations are unequal, then net transfers would occur across the membrane of the illustrative system.

Newman's comment on Read *et al.*'s shading treatment result is that 'A severely shaded plant might be expected to provide the greatest "demand" for organic carbon.' This is consistent with his illustrative system, but contradicts the thesis that net resource transfers do not occur. Fischer Walter *et al.* (1996), working in a natural prairie, found significant differences between species of receiver plant in uptake of labelled phosphate from a canopy dominant donor. The ratio of donor to receiver shoot mass was not a significant predictor of uptake, however, from which they concluded that inter-plant nutrient transfer via VA mycorrhizal fungi are *not* governed by source-sink relationships.

14.3. Suggested effects of direct transfers in plant communities

Grime *et al.* (1987) measured ^{14}C radioactivity from (donor) canopy dominant *Festuca ovina* L. in 10 receiver species, finding significant amounts in all nine VAM-associating species, and a highly significant reduction in yield of the donor (but not of a non-mycorrhizal control species) in mycorrhizal treatments. All species had been grown together in microcosms, and one effect of mycorrhizal infection was to reduce the dry weight of the canopy dominant by one third. On the basis of this result the authors suggested that 'export of assimilate from "source" (canopy dominants) to "sink" (understorey components) through a common mycelial network may be an important element of the mechanism maintaining species-rich communities in infertile soils.'

Newman (1988) suggests that the donor's yield reduction could have been due to mycorrhizal infection promoting growth of certain species better than others, but this formulation is vague. If the donor's yield is reduced only because the recipient species are able to compete (*sensu* Grime 1973) more when VAM-infected than when sterile, then one should expect a similar reduction in the yield of the non-mycorrhizal species present (which did not occur).

14.4. Suggested implications of direct transfers for theory

Here may be the opening shots of a great debate. Newman (1988) clearly realizes that if the case for net transfers is proven then a new paradigm - *of cooperation in plant communities* - will be needed when he concludes: 'Ecologists have for many years viewed relations between living green plants as primarily competitive, and the transfer of nutrients from one to another as occurring when one plant, or part of it, dies. I see no clear evidence that mycorrhizal links prevent these relationships from occurring or introduce fundamentally new interactions between plants.'

Grime *et al.* (1987) sketch how such cooperation could be in the donor's interests, suggesting that its *offspring* could benefit by being a recipient during establishment. I shall return to this point later.

Chapter 15. Cooperation between green plants: initial evolution

Having laid the groundwork, I am ready, in this section, to begin dealing with the question of plant-plant cooperation mediated by VAM fungi. Fig. 6 represents schematically a plant-fungus association. Fig. 7 depicts two plants connected by the same fungal hypha, and is seen to contain two plant-fungus associations.

15.1. Resource trading between green plants: cooperation vs competition

Liebig's Law of the Minimum states that the growth of a plant is *limited* by the availability of only one resource. If this limiting resource is subsequently supplied (by fertilizer addition, for example) then *another* resource begins to limit growth. The concept underlying this is that a given plant requires resources for growth in more or less *fixed* proportions. The total amount of each resource which it is therefore *able to use* out of any particular mixture of resources which happens to be available to it is dictated by the availability of the one resource which has the smallest ratio of (amount of that resource available)/(amount of that resource required per unit growth). Liebig's law is not quite true, plants having some flexibility in requirements, but it is a good approximation. It is generally referred to a long time-scale: a crop's growing season; but its logic will be equally applicable to the short term (say one day). Over short time scales or distances, the resource limiting growth is likely to vary to some extent. Organic matter (faeces, dead animal bodies etc.) may suddenly arrive at the soil surface; a (downwardly) drying soil profile may limit the availability of nitrogen²⁷; a grazing animal may suddenly reduce the rate at which it can fix light energy etc.

15.2. A 'thought experiment' to determine if cooperation is compatible with competition

I want now to pose a simple question: *if* a plant *could* trade resources with neighbours, would it be in its interest to do so?

Assume that a group of unrelated neighbouring plants have some linking infrastructure such that any one of them *is physically able* to trade resources²⁸ with any of several others²⁹; and also that their growth rates at any one time are sometimes limited by different resources' availabilities.

²⁷ Because soil nitrogen is nearly all organically bound and concentrated in the surface horizons, and the rate at which it can diffuse through water surface films decreases as soil dries.

²⁸ Assume also that they possess any information-processing capability which is necessary.

²⁹ A reasonable assumption, I will argue below, if they are linked by VAM fungi, since each does trade resources with the fungi, and the fungi do trade with others. There might, of course, be an 'overhead' cost involved for maintainance of the fungi, but this does not materially affect my argument.

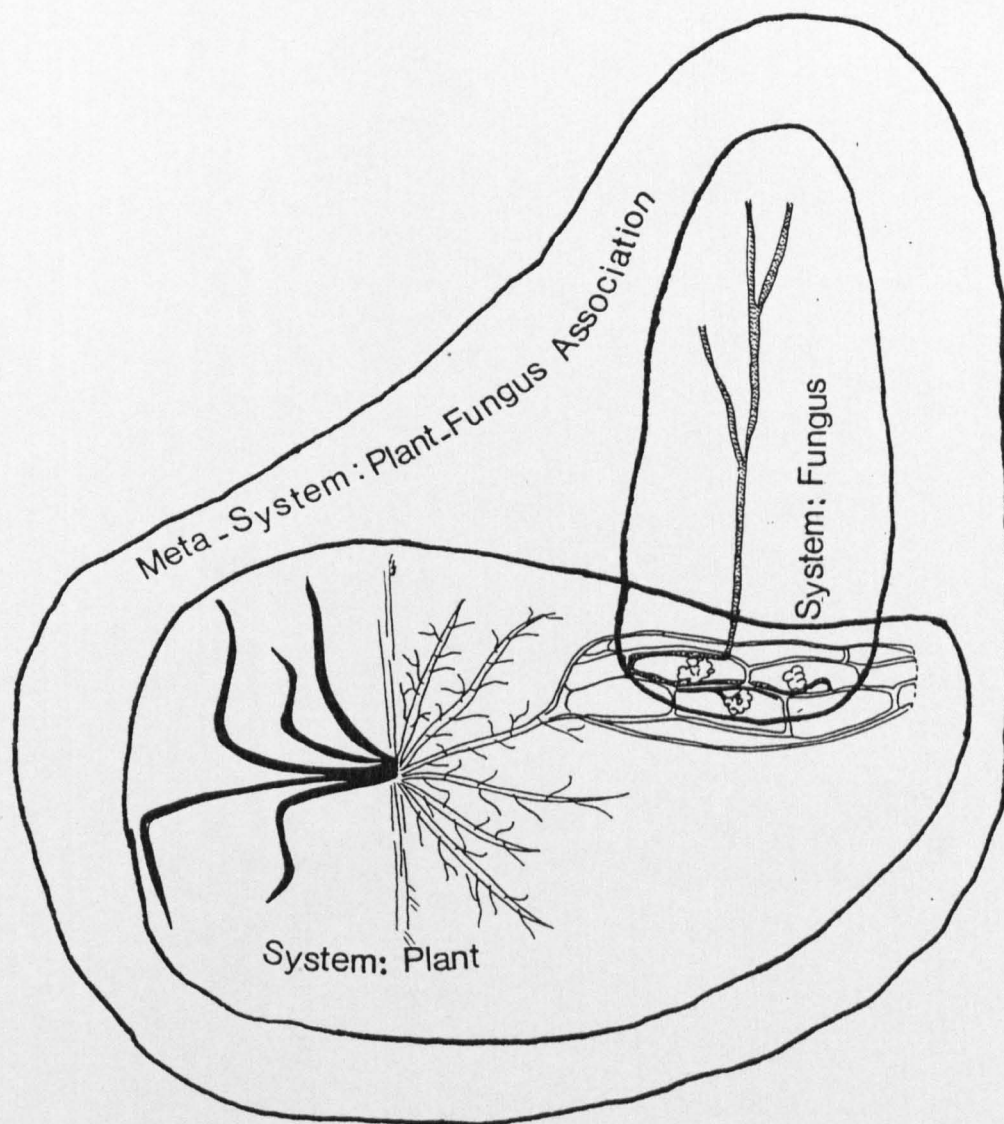


Figure 6. A 1:1 interaction. The plant and fungus, both systems themselves, are also components of a meta-system: a plant-fungus association.

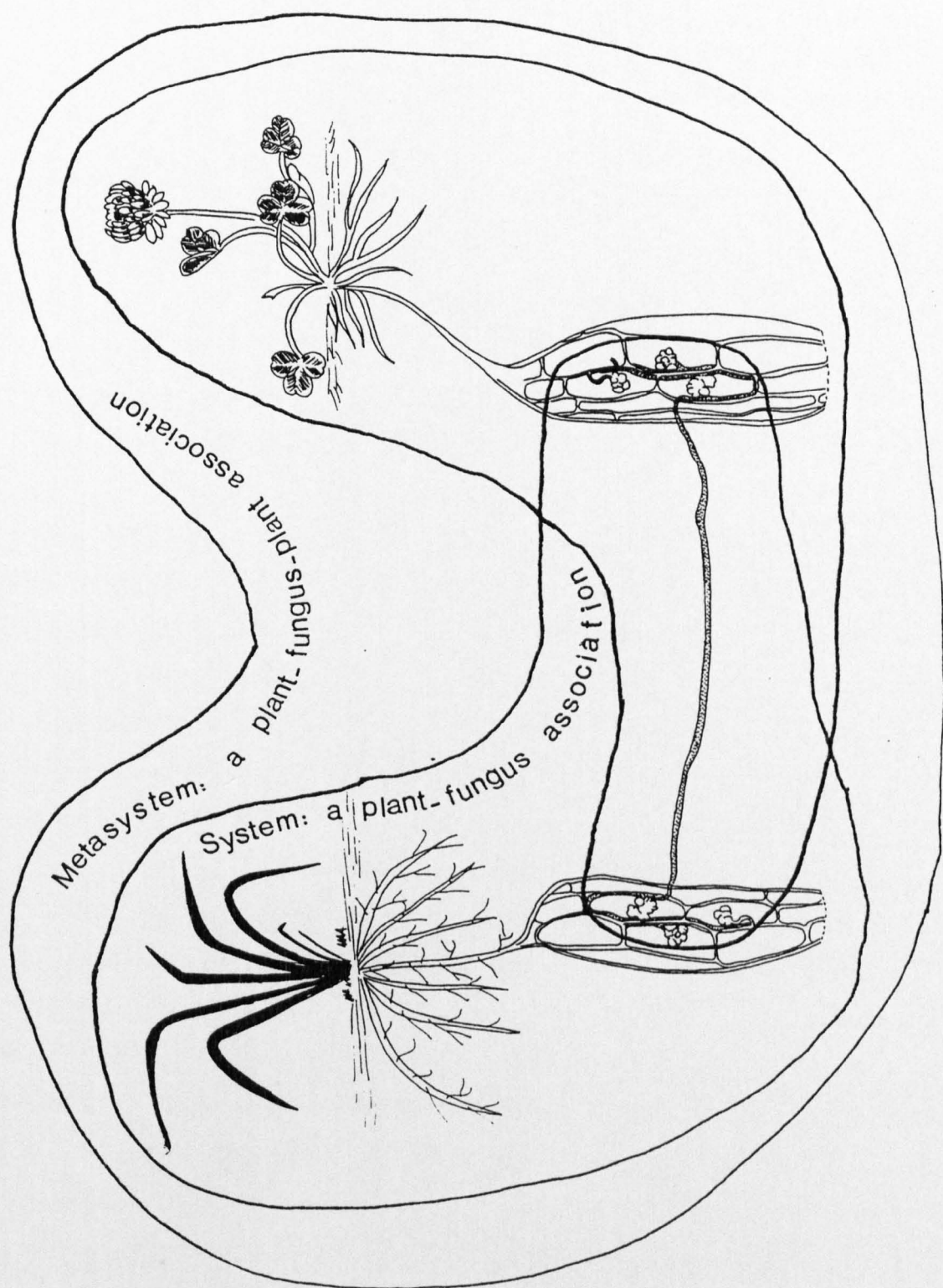


Figure 7. A 1:1:1 interaction. Two plant-fungus associations, linked by a common fungus, form components of a higher meta-system: a plant-fungus-plant association.

The question is: *would* it be to the mutual benefit (of the fitnesses) of any fungus-linked pair of them *to* so trade each a non-limiting resource in exchange for its limiting resource at a particular time when the growth of each is limited by a different resource? On the one hand each member of the pair of plants would, by Liebig's law, stand to gain in terms of its own growth. On the other hand it would, by trading, cause increased growth in the neighbour *with which it is in competition for resources*. From the resultant increased competition from that neighbour it should be expected to suffer a future *disadvantage*. It is thus clear that there is both a benefit and a cost associated with the trading of resources.

However, one reason for resistance to the idea that neighbouring plants could cooperate may be an assumption that cooperation and competition are somehow mutually exclusive: it must be against one's interests, as a competitor for the same resources, to strengthen a competing neighbour by cooperating with it. It is important to my argument to dismiss this assumption.

In aiding the growth of a neighbour, a plant is likely (let us presume certain) to be causing an increase in the competition for resources (*sensu* Grime, 1973) which that neighbour will exert against it in the future. However this would *not* necessarily prevent the transaction from being mutually beneficial. If both plants gain in growth equally, then neither is gaining competitive *advantage* over the other. Both, on the other hand, do stand to gain some competitive advantage over other neighbours which are not parties to the trading transaction. Trading would therefore be beneficial if it were possible. Even if the situation is that all the plants in a neighbourhood have such trading relationships with each other, the optimum decision on whether to trade or not will, in each particular case of a transaction, still be governed by the same rule: each transaction benefits both the transacting plants above their other neighbours³⁰. In fact the plant that does best out of trading will therefore be the one that manages to trade the most³¹.

The thought experiment has yielded a straightforward, if perhaps unexpected result: that if a plant *were* able to cooperate with a neighbour by trading resources then to do so would increase both its ability to grow and its size when compared with those of the totality of its neighbours. It seems an entirely reasonable supposition that this would normally confer

³⁰ Notwithstanding that cooperation and competition are compatible, the cost/benefit ratio of cooperating with a neighbour may improve with increasing distance from that neighbour.

³¹ Although it is irrelevant to my argument, I am not actually convinced that this situation would be necessarily to the advantage of the group cooperating plants as a whole. Although any plant not cooperating would presumably be at a disadvantage thereby, it is possible that the net result for the whole

increased fitness upon it. It follows that *if* a plant were able to begin trading resources then evolutionary pressures would favour the behaviour.

Aarssen and Turkington (1985b) presented the argument that two neighbouring plants may simultaneously be competing in one respect whilst cooperating over another; but the result from the thought experiment above allows the same resource to be simultaneously the subject of competition and cooperation. This finding is important to my case. Having established that *if* plants could cooperate they would; I can now turn my attention to the question how might plants be able to cooperate?

15.3. Two plant individuals cooperating with the same VAM fungus

In this section I will carry forward my argument by using what I have previously deduced about the *structure* of the relationship between a plant and associated VAM fungus; asking the following question. *What are the implications of that structure for the case of two green plants which happen to be linked by a fungus?*

We need to conceptualize the situation of two plants which are linked together by a single fungus. How would Game Theory describe the situation of a plant *A* cooperating with a fungus which is itself at the same time cooperating with another plant *B*?

Let us presume in the first instance that plant *A* cannot recognize the presence of the indirect partner plant *B*³². Plant *A* is then in the position of playing against a single partner, being only able to respond in its plays to previous plays of the fungus - not those of plant *B*. These plays of the fungus (to which plant *A* responds) will, however, be altered by the existence of the fungus' association with plant *B*. The single partner which, from its viewpoint, plant *A* plays against is thus actually composite, consisting of the association of the fungus with plant *B*. Meanwhile plant *B* is in exactly the same position as plant *A*.

It could be argued that this situation represents already a type of cooperation between *A* and *B*. The fungus, presuming that it is benefitting from its association with *B*, has more resources at its disposal than it would have in the absence of *B*. The possession of these extra resources is likely to *enable* the fungus, *but does not compel* it, to be a more beneficial partner for *A*. However, as I have already argued, the plant is able to select the more beneficial from a population of mycorrhizal fungi. Therefore (plant-mediated) natural selection among the population of dually-associated fungi will tend to favour those mutant strains which fulfil their potential to be more beneficial.

plant community would be a larger cost in terms of maintaining the VAM network than profit from mutual trading with each other.

³² This might be seen as representing a common situation once the VAM-plant symbiosis had evolved - see below for discussion of the alternative assumption.

The VAM fungus, which makes its living by trading resources, is in the position of having increased possibilities of trading resources gained from a plant to a plant, and not only soil-gained resources (mainly P) for plant resources. Provided that the relative resource costs of each resource's production are not identical in each plant, then both plants can gain by a redistribution, and from this gain to the plants, the VAM can take a proportion (thus benefitting from the dual association), yet remain itself beneficial (which is, as I hope I have shown, necessary to its own evolutionary success).

The plant is in the position that it is benefitting from the trading of resources with a composite partner which includes a neighbouring green plant. If we describe the plant-fungus association as mutualistic, should we not apply the same adjective to the relationship between the two plants?

The type of cooperation between green plants described above I conceive as ancestral. It could be termed 'interface-based cooperation' since a green plant player is only able to recognize, and therefore play against, the *interface* (i.e. the fungus) separating it from a green plant neighbour - not the neighbour itself.

The existence of inter-plant cooperation may have begun with two plants each cooperating simultaneously with the same mycorrhizal fungus. Consider such a trio constellation of two plants and one fungus in which the fungus possesses the only uniting control system: what evolutionary possibilities are offered in this situation to the plant genome lines? From the initial position that each cooperates only with the fungus what is the scope for them to evolve to a closer, more direct relationship in which the fungus becomes the vehicle of *their* cooperation with each other? The trio (and upward) is a new field of evolution, waiting for the grasp of science.

Chapter 16. 'Direct' nutrient transfers and biotic specialisation

In this chapter I return again to the first published model of plant-plant cooperation of which I am aware - that put forward by Grime *et al.* (1987).

16.1. 'Direct' nutrient transfers - can canopy dominants donate resources to benefit their offspring?

Grime *et al.* (1987) suggest that *Festuca ovina*³³ may donate photosynthate to neighbouring plants *via* shared mycorrhizal fungi³⁴, and that this may be in their interests because their offspring could benefit by being recipients during establishment. It was through consideration of the postulates necessary to support this suggestion that the present study was conceived: there seemed to be problem with it.

If the authors mean to imply that, of the resources donated by a *Festuca ovina* individual, a portion goes directly to its own offspring, and it is *only* this portion which increases its fitness, then this would seem a very inefficient way of 'handing down' resources to the succeeding generation - as compared with investing the same resource in larger seed or vegetative propagules instead. The offspring, being initially small and thus possessing a small root system, might be expected to have relatively few linking mycorrhizal connections in comparison with other neighbours. The resource donations received by these other neighbours would be likely to increase the competition for resources which they exerted against it.

If, on the other hand, Grime *et al.* have in mind that the *F. ovina* plant is donating resources to a network consisting of neighbouring plants and mycorrhizal fungi, which *network* reciprocates by supporting the establishment of the donor's offspring, then some further explanation is required: mutual benefit *at the species level* may be conceded; but this is an insufficient condition for cooperation to exist, as in the case of cooperation between a VAM fungus and a plant, discussed above. A mutant *F. ovina* genotype which benefits from the network's help when establishing and then fails to return it when established would render the strategy of helping *F. ovina* seedlings unstable. Such

³³ And likewise canopy dominants in general (Grime *et al.* 1988).

³⁴ A preferable formulation of this hypothesis might be to posit that canopy dominants bear a disproportionate share of the energy costs of maintaining the whole system of plants and associated mycorrhizal fungi. Newman (1988) points out that one green plant could aid another by supplying photosynthate to a shared mycorrhizal fungus, which might then supply phosphorus to the second without requiring photosynthate of it. Such a situation should still be seen as a type of resource donation by the first plant to the second.

defection is made possible by the control which, I have argued, plants *must* have over their symbiont fungi for the formation of such associations to remain (as they clearly do) evolutionarily stable: this is not a system governed by source-sink relationships between the cytoplasm concentrations of the protagonists³⁵.

In sum, Grime *et al.* observed subordinate plants of other species apparently benefitting from resource donations made by *F. ovina*, the canopy dominant, at considerable expense to itself. What is required to allow existence of a such a reciprocal cooperative relationship between a canopy dominant and neighbouring subordinates through their associated mycorrhizal fungi? We must accept that they cannot aid each other from sheer, as it were, optimism that cooperation will be reciprocated. Rather, they must establish particular relationships with each other through repeated encounters, and in particular the subordinates would have to be able to recognize the dominant's offspring as related to it.

16.2. Biotic specialisation - Some evidence of advantage conferred by neighbour familiarity

Is there any evidence that plants are indeed able to recognize past partners? The results of Gliddon and Trathan (1985) merit attention.

They noted that local specialisation had been demonstrated by a number of studies in which ecotypes were shown to exist which were a consequence of the biotic, rather than the physical, components of the environment. What had brought about such local specialisation was not clear but individuals' growth rates had been strongly influenced.

If local specialisation were a genetic component of fitness, rather than an environmental conditioning, they expected to find differences in local gene frequencies within a species. If this occurred in more than one species, there might be correlations between the genotypes of different species.

They set out to investigate the population genetic structure of *Trifolium repens* L. and *Lolium perenne* L. by, firstly, an electrophoretic survey and genetic analysis of population structure using marker alleles; and, secondly, a direct examination of the existence of local specialisation using reciprocal transplantation techniques and competition experiments.

³⁵ Although the theory I am developing here predicts that resource transfers are often likely to be made in the same direction that a simple source-sink dynamic would cause, since a low cytoplasm concentration of a resource is likely to indicate a requirement for that resource.

16.2.1. The vegetation survey

They carried out a vegetation survey to select sites which were similar for use in the electrophoretic survey and to observe changes in the field over time.

Of their genetic analysis of population structure using marker alleles they wrote 'The attempt to find genetic correlations between the two species consisted of a Canonical Correlation Analysis. No significant correlations whatsoever were found.'

16.2.2. The transplantation experiment

From each of four sites used in the vegetation survey they picked four genotypes of each species at random and propagated from them. They divided the four transplant sites each into four replicate blocks and planted an individual from each of the 16 clones of *T. repens* and the 16 clones of *L. perenne* in each block. 98% of *T. repens* transplants survived in familiar sites as against 34% in alien sites; *L. perenne* mean dry weight was 0.30g for familiar, as against 0.19g for alien transplants.

16.2.3. The competition experiment

They also performed a competition experiment in pots to eliminate site effects. Picking four neighbour pairs of the two species and propagating from them vegetatively, they planted eight tillers in a circle and, after allowing them to establish, introduced a rooted stolon tip of *T. repens* into the centre of the pot. This was done in all pairwise combinations of the genotypes³⁶.

There were no effects of clover genotype on ryegrass genotype as had been envisaged by the authors³⁷, but a significant effect of ryegrass on clover yields was shown.

Thus they were successful in their attempted elimination of site effects. This being so, it is clearly incorrect to call the effect 'local specialisation', and 'biotic specialisation' is now more often used.

16.2.4. The authors' interpretation of results

The authors were exploring the boundaries of a recently discovered effect and they freely admit that 'the mechanism by which local specialisation arises is unclear'. Suggesting that nearby sites may be substantially genetically isolated from each other, they posit that

³⁶ It is unfortunate that much work in the field suffers from an inefficiency in experimental method. The *fully* factorial design limits the number of origins which can practically be permuted to about four, and leads to a preponderance of alien over familiar treatments.

³⁷ Perhaps unsurprisingly in view of the 8:1 majority of *L. perenne* plants and their advantage of earlier establishment.

this 'would allow either locally varying selection or genetic drift to give rise to microevolutionary differences between sites'.

16.2.5. Genetic drift

The term 'genetic drift' was coined by Wright (1951) to refer to random genetic change occurring by the survival of *selectively neutral* mutations. On this definition it cannot be correct to invoke the term to explain what appears an obviously adaptive phenomenon.

16.2.6. Locally varying selection

Gliddon and Trathan (1985) set out to test a hypothesis: 'if local specialisation is a genetic component of fitness, rather than an environmental conditioning, one would expect to find differences in local gene frequencies within a species, that is population sub-division, and, if this phenomenon occurs in more than one species, there may be between-species correlations of genotypes.'

Yet they did not accept the clearly negative results of that test when 'no significant correlations whatsoever' were found. Instead they persisted in suggesting that a microevolutionary explanation can account for their results. Quite apart from contradicting their own finding, this seems too vague to be tenable. 'Microevolution' *affecting what characters? driven by what selective pressures?*

The only characters that spring to mind as possible candidates here are depth of rooting (or, similarly, above-ground growth habit). One might imagine that two plant neighbours could both benefit if they had been able to evolve different rooting habits so as to use different soil volumes and thus reduce competition. There is, however, a problem with this. A plant has, usually, not one but several neighbours, each of which, in turn, also has several other neighbours. Even if an evolutionary 'fast track' existed for the rapid alteration of rooting habit it appears unlikely that a genome line's environment could present it with sufficiently clear feedback to allow the evolution to take place. Given several neighbours each with different rooting depths a plant could not have a rooting depth which is complementary to all of them; and on what basis could it develop complementarity to one neighbour only, ignoring the equivalent selective pressures exerted by the other neighbours? A similar argument applies against the possibility of any other kind of complementarity of resource use which might be offered as an explanation of 'local specialisation'.

A further point about the Microevolution Hypothesis: if this were the true explanation of their results one might expect that *T. repens* genotypes adapted to 'fit' different *species* of grass would differ more than *T. repens* genotypes adapted to 'fit' different strains of one grass species from the same field. This greater difference should be expected to result in

different (familiar *versus* alien) *species* of grass having a greater effect on yields of clover transplants than would different (familiar *versus* alien) *strains* of one grass species.

Published results can be used, albeit imperfectly because of incomplete data, to compare the familiarity advantage enjoyed by *T. repens* in trials with different neighbour grass species *versus* that in trials with different genotypes within the same grass species. Results are that the means of both (taken from six papers plus my own results) are similar (see Table 9).

An additional reason for rejecting evolutionary explanations comes from Gliddon and Trathan's observation that 'the vegetation in the field changed sufficiently from season to season to result in completely different sets of sites being grouped as similar in the vegetation classification for different seasons.' This strongly suggests that the plants may not have been neighbours for long enough for natural selection to operate³⁸.

16.3. Other interpretations of biotic specialisation

What should we conclude from Gliddon and Trathan's work? They observed a phenomenon in which site factors were not involved³⁹, whereby plants benefitted, in growth or survivorship, from being planted among erstwhile neighbours or their vegetative offspring. This is to say that

- a) Plants can develop *something* which is specific to neighbouring plants of other species.
- b) From this *something* they are able subsequently to benefit.

The authors' attempted explanations for this - which rely on the operation of evolutionary processes over short timescales - are unsatisfactory.

I suggest that this something is cooperative relationships involving 'direct' resource transfers. Gliddon and Trathan's results support the hypothesis that *T. repens* and *L. perenne* plants form cooperative relationships with individuals of each other's species; that such relationships are able to persist through vegetative generations; and that they confer increased fitness on the vegetative offspring of neighbour plants⁴⁰. It is interesting that this

³⁸ Their raw data would shed more light on this - they do not say which species were changing frequency in their sampling squares.

³⁹ 'Local specialisation' is an inappropriate term since Gliddon and Trathan (1985) eliminated site factors. See below.

⁴⁰ Note that the authors' explanations imply that only a plant itself has changed in some way as a result of exposure to a particular neighbour. My interpretation contrasts with this in postulating that the effect is intrinsic to both plant and neighbour.

Table 9. Meta-analysis of familiarity advantage due to neighbour species *versus* that due to neighbour genotypes.

Note: Familiarity Advantage = FA = (Y(f) - Y(a)) / Y(a); where Y(f) and Y(a) are *T. repens* shoot dry weights in familiar and alien treatment respectively. Values greater than zero mean the familiar treatment is advantageous.

A. Familiar Genotype Advantage

Source	mean Yf	mean Ya	FA
-----+-----+-----+-----			
2) Tab 2	3.23	1.62	1.00
3) Fig 17.6	7.93	6.21	0.28
6) Tab 6	3.183	2.01	0.59
7) Tab 10	3.065	2.73	0.12
Overall Mean			0.50

B. Familiar Species Advantage

Source	mean Yf	mean Ya	FA
-----+-----+-----+-----			
1) Tab 1b	0.89	0.52	0.73 (replanted to field)
1) Tab 1c	59.35	31.95	0.86 (planted to sown swards)
3) Fig 17.4	6.84	6.96	-0.02
4) Fig 3	6.78	6.08	0.11 (Brit. Col. meadow)
5) Tab 4a	1.8	1.07	0.69 (Henfaes)
Overall Mean			0.47

In the above, only *T. repens*'s homologous *Rhizobium* strains are included, where others exist. All *Rhizobium* treatments for 6) Fig 3 give:

B. Familiar Species Advantage

Source	mean Yf	mean Ya	FA
-----+-----+-----+-----			
4) Fig 3	6.67	6.49	0.03 (Brit. Col. meadow, all <i>Rhizob.</i> treats.)

Key to Sources:

- 1) Turkington & Harper 1979
- 2) Aarssen & Turkington 1985b
- 3) Turkington et al. 1988
- 4) Thompson et al. 1990
- 5) Turkington 1989a
- 6) Gliddon & Trathan 1985
- 7) This thesis

NOTE: Source 5, alone, has both species and genotype results.

cooperative relationship, if such it is, cannot be underpinned by recognition at the level of particular plant-fungus interfaces, which is what Axelrod and Hamilton (1981) suggest as

the basis of plant-mycorrhizal fungus cooperation. If recognition were thus 'interface-based', then benefit from the relationship with a neighbour plant would not persist after the breakage of these links and cloning in the laboratory for six months.

However, further work has been done and other hypotheses advanced to account for the phenomenon of biotic specialisation, which I will deal with before elaborating on the suggestion that VAM fungus-mediated IPD cooperation could be responsible.

Most of the literature on biotic specialization has contrasted different species rather than different genotypes within a species, and is thus not directly relevant to my work.

Nevertheless, I should point out that the theory of inter-plant cooperation which I am putting forward here is able to encompass biotic specialization to different species: if an individual has an ongoing cooperative relationship with a neighbour of another species *X* and is then transplanted into experimental plots with companions of one of several other species *X*, *Y* and *Z*, it is plausibly a good game strategy to be more cooperative with *X* than with *Y* or *Z*. This is because *other* individuals of *X* (in the same neighbourhood, as far as the plant is concerned, because ramets do not naturally become transplanted far from their origin) are 'known' to be cooperators and this will weight the predicted payoff matrix in their favour.

There is a problem with the species-specialization papers in that they tend not to make clear the spatial relationships between their field-sampled material - are the species *A* individuals found by experiment to be adapted to species *B* taken from the same or different neighbourhoods as the species *B* individuals they are grown with experimentally?

Turkington (1989a), like Gliddon and Trathan (1985), argues for a genetic basis underlying some of the "local specialisation" effects reported in the literature (Turkington, 1989a; Turkington & Harper, 1979; Burdon, 1980; Evans *et al.* 1985; Gliddon and Trathan, 1985). However:

- a) He points out that this cannot explain all the reported results since two studies (Aarssen & Turkington 1985b; Evans & Turkington 1988) are from a meadow in British Columbia where the patches are too small - "most patches are probably less than 1 m²" - for there to exist any possibility of evolution occurring within a patch. This represents a change of view, compared to that expressed by Aarssen and Turkington (1985a).
- b) Plants taken from the British Columbia meadow, which had differing phenotypes in the field, became morphologically similar over a period of two years growing in the same environment - a common garden - Evans & Turkington (1988), suggesting that the different 'genotypes' studied may not in fact have been different genotypes at all

with respect to the morphological characters according to which they were classified. Rather, their difference may reflect phenotypic plasticity.

- c) The other studies were mostly done in the same North Welsh meadow, in which patches are larger (up to 150 m²). Yet, of these, Gliddon and Trathan (1985), although claiming a genetic basis, did so without justification and contrary to their own results.

If micro-evolutionary explanations are accepted for biotic specialization in pastures where such a thing is conceivable (on the basis of large patch sizes) then *another*, non-evolutionary, explanation is required for the other cases, and it would be more parsimonious to accept inter-plant cooperation as a single theory able to explain both cases.

Biotic specialization to different species is apparent in the British Columbia meadow, where micro-evolutionary explanations cannot be countenanced. A theory of inter-plant cooperation can explain this; but even if this should be disproved we are still in the interesting situation of needing some other kind of explanation involving a *facultative* change in plant behaviour in response to the identity of its neighbours.

16.3.1. Niche differentiation

The phenomenon of biotic specialization is sometimes explained as due to niche differentiation, but this seems nebulous. Proponents don't specify, operationally, what resources they are talking about or how the plant might withdraw them from its environment in a different temporal or spatial pattern. One is left thinking that rooting depth or, a little more precisely, the vertical profile of the root system, is the only obvious possibility if they are talking about nutrients. But how many distinct and different profiles can one species' root system exhibit? Not very many, one would think. One would therefore expect that, given only a moderate number of neighbourhoods from which neighbouring pairs of *L. perenne* and *T. repens* are sampled, some of the alien pairs would do as well as the familiar ones. This would be testable.

Two other problems with the niche differentiation explanation are the fact that most plants have more than one neighbour (see above) and the fact that changing the root profile may only have a limited effect on the degree of competition exerted since nutrients tend to travel down the profile in solution - i.e. the soil profile is only partly a truly three dimensional resource space.

16.3.2. More balanced competitive abilities or reduction in competitive pressure exerted by *L. perenne*

What is the meaning of (Aarssen and Turkington (1985b) "This study suggests that natural selection, in contexts of competition, may result in more balanced competitive

abilities for contested resources instead of niche differentiation"? What, *operationally* are "more balanced competitive abilities"? If these authors mean *forbearing* to compete with a neighbour for nutrients then this suffers the problem that *other* neighbours will also benefit - to the future disbenefit of the focal plant. How would a plant detect defection? Such a mechanism looks too crude to succeed, but it seems to be tending towards an explanation involving some form of cooperation. If the authors do not mean that neighbours may *forbear* competing with each other then are they assuming that the plant competes *to the limit* of its 'abilities' to do so and it is *those abilities* which are reduced?

If the plant does not compete to the limit of its abilities then what is the structural linkage between the resource flow that the plant *could* import and what it *does* import? *I.e.* What factors lead it to compete less than it could? If it does compete to the limit of its abilities, on the other hand, then it is a little hard to see how a reduction in its competitive abilities is appropriate adaptation when environmental stress has not increased. In any case a (plastic or evolutionary) change towards stress-tolerance would surely not result in such specific adaptations to particular neighbour species and genotypes as are found.

Aarssen and Turkington (1985b) also posit a reduction in competitive pressure exerted against neighbouring *T. repens* by *L. perenne*: "Grass genets which ultimately leave the most descendants may... be those that are competitive enough to avoid exclusion by the clover, but are not so competitive as to suppress or eliminate the source of nitrogen made available by a neighbouring clover. This may be especially important to fitness if available soil nitrogen is scarce."

A question thus arises could IPD cooperation work through the soil matrix material instead of through VAM hyphae? In principle the possibility is apparent; a plant's plays would consist of exerting strong or weak (even negative) sinks for any nutrient of interest (*i.e.* in minimum) through its roots, and a strong sink would constitute a play of Defect, a weak or negative sink a play of Cooperate.

It might be argued that such matrix-mediated cooperation has the advantage over VAM-mediated cooperation that the resource cost of supporting VAM fungus would be avoided. I think, however, that other factors will outweigh this consideration and render matrix-mediated cooperation less efficient than VAM-mediated cooperation - very possibly to the point of non-viability. These factors are:

- a) The plant is likely to need VAMs in any case for soil nutrient extraction - especially if it is a stress-tolerator, which, I have argued, is the type most likely to cooperate with its neighbours.

- b) The relevant factor is not simply the cost of exporting nutrient, but the ratio of *cost of nutrient export to the exporter to value of nutrient import to the importer*. Only if the value is greater than the cost can there be any benefit in the transaction. If some of the nutrient is lost in transit - either to a second neighbour or to (chemical or biological) immobilization processes in the soil - then the *value of cooperation received* by the first neighbour is reduced. Such losses seems inevitable.
- c) The increased difficulty of 'knowing' *which* neighbour has played Cooperate - or, indeed, if *any* play of Cooperate or Defect has in fact occurred. The receiving channel through which the neighbour gains the 'donated' nutrient is *open*. Whereas a VAM channel interface could carry both the nutrient and recognition chemicals, so that a receiving plant might 'know' the nutrient's provenance, the soil channel both makes it more difficult for the donor's recognition chemicals⁴¹ to arrive at the receiver's root surface (through the hungry rhizosphere population) and will also allow *other* plants' recognition chemicals through.

16.3.3. Mutualism based on a *L. perenne*-*Rhizobium* interaction

Aarssen and Turkington (1985b) and Turkington *et al.* (1988) are led, by a significant effect of familiar *versus* alien *Rhizobium* strain, to suggest that some kind of mutualism (whose form they do not specify very precisely) occurs between *T. repens* and *L. perenne*, and that the mechanism of this involves *Rhizobium*. "The genotype-specific coadaptation in local neighbourhoods may be further mediated by a complex indirect mutualism involving interaction of particular grass genotypes and particular strains of symbiotic *Rhizobium* in the clover".

However, Luescher *et al.* (1992) investigated this experimentally and found neighbour specificity even when the strain of *Rhizobium* used was alien to the experimental plants, which still needs explanation.

Moreover, what sort of 'complex indirect mutualism' might the *L. perenne* be involved in? Could they be *selecting* effective *Rhizobium* strains? or *priming* *Rhizobium* strains to be effective (with information or Vanadium, for example)? or placing *Rhizobium* where *T. repens* can find and use it? or exerting continuing *control* over *Rhizobium* even within the *T. repens* nodules? It is very difficult to imagine how any of these could happen.

⁴¹ I do not mean to imply that the recognition chemicals are 'designed' for this purpose by their producer's evolution; as with Lewis's (1986) algae, their significance need only be to the receiver.

Chapter 17. How far might cooperation have evolved?

None of the explanations put forward for biotic specialisation are without difficulties, and, although some, or perhaps all of them may be valid, there remains a hard residue of experimental fact which still needs to be explained by some other mechanism. The difficulties of micro-evolutionary explanations have been apparent to other workers than myself, who have also been driven by these difficulties to consider that mutualism of some kind seems to be involved.

However, the forms of cooperation which these workers have postulated also have problems. The reduced competition mechanism does not explain how a focal plant is able to recognise whether a beneficiary of its own play of cooperate has reciprocated, or how it might retaliate effectively if not, given that the soil matrix is also shared by many other neighbours simultaneously. The nature of the proposed mechanism involving *Rhizobium* is too unclear.

On the other hand it does seem possible that IPD cooperation could evolve and remain stable through the medium of VAM hyphal connections, because such direct-channel connections are precisely what is needed to fulfil the informational requirements of cooperation (recognition), at the same time as providing an efficient transport medium for resources (i.e. losses-in-transit could be low), which is also directed rather than diffuse.

One test of this *could* be simple in principle: does the effect still occur in the absence of VAMs? To test it more certainly would require that we measure not the *persistence* but the *development* of the effect in the presence and absence of VAMs.

I have argued (above) that it is logically necessary for the plant to be able to 'recognize' VAM fungal partners (if only by location) if the relationship is to remain mutualistic, and further argued that where two plants are involved in a cooperative relationship with the same VAM fungus, a type of indirect cooperation may be said, *de facto*, to exist between them. Further benefits of inter-plant cooperation would flow from increased ability to process information regarding partner recognition. In particular, it would benefit their fitness if they are able to recognize, and therefore play directly against, their indirect green partners.

Whether plants in fact do possess the ability to recognise partners is open to determination by experimental means, which will be addressed in a later chapter.

Having presented, in the last chapter, evidence that such an ability exists, here I will argue how it could operate, and discuss possible stages through which plants' partner-recognition abilities could have evolved.

17.1. Ability to distinguish connected vs unconnected VAM interfaces

It would seem to be a relatively simple matter for a plant to evolve the ability to detect whether a particular VAM-root interface is connecting it to another root: either by the detection of chemicals of green plant origin; or, possibly, by the different behaviour exhibited by the VAM which may have a different structure of resource needs and resource availabilities if it has a connection to another plant.

Such an ability to discriminate between VAM interfaces which are shared and those which are not would be beneficial to the plant since it would supply some information about how the interface is likely to behave in the future. That is, it could usefully inform play⁴².

17.2. Ability to distinguish self-connected vs other-connected VAM interfaces

The next, useful stage in development of plant perception of the VAM interface might be the ability to distinguish between two types of shared VAM: those reconnecting to another part of its own root system as against those connecting to other plants' root systems. The point of this is that different payoff matrices correspond to the two types of interface: there can be no hope of a self-to-self resource 'donation' being usefully repaid in the future.

17.3. Finer discrimination of other-connected interfaces: *by species*

This ability could be useful in two ways: firstly to enable better prediction of a partner's behaviour (thus allowing better game strategy to be played); and secondly it might use species recognition as a surrogate for individual plant partner recognition (see below). If it were in the survival interest of the genome line to evolve an ability to recognize the species of a neighbour, then this would not appear to be difficult since, firstly, plant roots are able to take up many organic molecules (Nye and Tinker 1977 page 128; Scott Russell, 1977 page 70); whilst, secondly, plants have evolved sophisticated recognition systems for identifying pathogens (Heslop-Harrison, 1978) and incompatible pollen types (Hodgkin et al., 1988). That the evolutionary step of species recognition has, in fact, happened is argued very compellingly by Lewis (1986) for phytoplankton whose growth behaviour varies in response to the presence of particular other ('trigger') species (see below). What would be the advantages of an ability to recognize the species of neighbours?

⁴² Therefore plants would be likely to exert selection pressure in favour of a mycorrhizal fungus which is able to thus deliver sufficient traces of recognizable metabolites.

17.3.1. To better predict a partner's behaviour

Recognition of the species to which a linking mycorrhizal fungus is connected could be useful because the ecological behaviour, and thence game-playing strategy, of a green partner is very likely to vary with its species as, also, is the probability of re-encounter with it and its offspring. Species recognition would give a genome line the opportunity to acquire instincts against cooperation with ruderal plants which, because of their 'here today, gone tomorrow' habit, should be expected to end any cooperative relationship by defecting⁴³. This would explain why VA fungal mycelia have a negative effect on ruderal plants, but a positive effect on 'K' selected ones (Francis and Read (1994).

Species will differ also in their chances of surviving environmental stress/disturbance⁴⁴. Again this information is potentially useful, since it becomes rational⁴⁵ to defect when a partner is going to be unable to cooperate further.

17.3.2. To recognize individual plant partners

Provided that the plant is able to integrate its information-processing capability at a higher level than that of individual VAM interfaces, the ability to recognize individual plant partners would represent a very important development of the plant's capacity to process information. Instead of playing separate games against many individual VAM interfaces, the plant would now be able to play directly against a particular neighbour⁴⁶. As well as being able to base its plays on much better information, the plant would, paradoxically, also need less information-processing capacity in order to do so.

Because many plants live in diverse communities, with neighbours of several different species, a high degree of this ability to recognize an indirect (i.e. green plant) partner would be gained simply by the ability to recognize the *species* to which a dually-connected VAM interface connects. In the case where the plant has only one neighbour of a particular species, then the mapping is perfect, and species recognition constitutes precisely recognition of the individual partner. Even where the plant has more than one neighbour of the particular species there is a chance that they may be closely related to each other. Such

⁴³ Non-mycorrhizal plants are most commonly found in disturbed habitats. (Newman, 1988).

⁴⁴ Whether an environmental factor such as drought constitutes stress or disturbance (*sensu* Grime, 1973) is, of course, a quality of the plant being affected, rather than a function only of the factors own parameters. A certain degree of drought will kill one plant, but merely slow the growth of another.

⁴⁵ A Game Theoretic term meaning optimal.

⁴⁶ One way of looking at this is to see it as a way of increasing w by reclassifying mycorrhizal interfaces according to the green plant partner with which they connect: greatly reducing the number of partners and

relatedness would help the plant in two ways: firstly because the more closely they are related the more likely is it that their game strategies will be similar; and secondly because aid (or defection) mistakenly afforded to the wrong partner⁴⁷, will nevertheless be contributing to the fitness of genes shared by the correct partner.

Is the evolution of an ability to distinguish the species of an indirect plant partner plausible?

17.3.3. Species recognition among phytoplankton

Lewis (1986) argues persuasively that the allelochemistry of phytoplankton algae cannot be, as has been conventionally assumed, allelopathy (i.e. one organism producing chemicals to suppress another organism) on the logical grounds that, for several reasons: 'the benefits of [an allelopathic metabolite] are not captured either uniquely or even with significantly higher probability by the cell that produces the metabolite; rather, the benefits are distributed among many cells. This inevitably creates an advantage for any cell that is of similar genetic constitution to the releasing organism but does not synthesize the allelochemical. Such a 'cheater' saves the metabolic cost of the allelochemical while benefitting from its production by other cells. Thus, for phytoplankton cells, the production of allelochemicals as agents of interference competition is not an evolutionarily stable strategy.'

The evidence for the conventional view consists of laboratory studies of two-species mixtures of phytoplankton which do not co-occur in nature, and at much higher concentrations than are natural. A laboratory study reproducing natural conditions in a pond (Keating 1977) found consistently that 'metabolites produced by a given species were in all instances either repressive or neutral to species occurring earlier in the sequence, but were either stimulatory or neutral to species occurring later in the sequence.' (Lewis 1986).

Rather than being significant to the *releasing* organism, Lewis considers that these 'allelochemicals are significant *to the receptor organism* as cues that trigger physiological responses to an improving or deteriorating environment', allowing them to recognize the presence of algal species which precede them in the succession. He comments: 'The allelochemical-signal hypothesis credits phytoplankton cells with physiological recognition mechanisms, implying that cells contain a certain amount of physiological programming based on environmental cues.'

increasing the number of interactions with each (by the number of mycorrhizal interfaces connecting with each).

⁴⁷ I.e. plays directed at neighbour B as a result of previous plays received from neighbour A.

Thus even so early a life form as phytoplankton algae are capable of recognizing another species' presence by sensing one or several metabolites which are specific to that species, responding to such stimuli by switching growth on or off. This can be seen as equivalent to a sense of smell.

17.3.4. Species recognition among higher plants

Heslop-Harrison (1978, p51) supplies an example of higher plants recognizing the presence of particular species: 'Several root parasites have evolved methods of detecting the presence of potential hosts. Good examples are provided by species of *Striga* (witchweeds: Scrophulariaceae). [...] The seeds of the parasite germinate best in the vicinity of the host roots, and this is due to the presence of promoting substances in the root exudates. One of these, strigol, a highly potent factor from cotton (*Gossypium* spp.) roots, has been isolated and characterized.'

It seems far from impossible that a cooperating higher plant might similarly recognize the species of a neighbouring plant through its metabolites arriving at a mycorrhizal fungal interface.

17.4. Distinguishing within species of connected plant

Any significant degree of discrimination *within* species would be likely to increase the extent to which a plant could play directly against connected plants, instead of against fungal interfaces, thus increasing w . However, a considerable further increase in fitness could result from evolution of the ability to distinguish between connected plant partners on the basis of *whether or not some parent or close relative has been previously encountered*⁴⁸. Such an ability would increase w by enabling game play to span generations instead of needing to start afresh with each new individual. Bearing in mind the short distances of dispersal of vegetatively 'reproducing' plants, the resultant ability *to influence the behaviour of neighbours towards one's offspring* through one's game plays would be likely to be important; and *this* could be a basis for canopy dominants to be able to supply resource to neighbouring subordinates, as Grime *et al.* (1987) suggest, with some expectation of a payoff (but see a further suggestion below).

⁴⁸ What could be the basis of such recognition *within* species? Since it is better game strategy to choose to play against a recognizable individual, it will be in the interests of a cooperator to be recognized. A high mutation rate in genes controlling production of allelochemical signals might therefore increase fitness by supplying a basis for recognition. Another possibility: Sutherland and Watkinson (1986) suggest that 'somatic mutations will produce enough variability to prevent pathogens and herbivores from adapting to all branches on individual host trees'. Such variability might also supply the difference between individuals necessary if they are to be discriminated.

There is another side to this matter. In the human world, the most valuable cooperative relationships are those which have been tested by life-threatening episodes ('a friend in need is a friend indeed', says the proverb). The more serious of these do not occur in every generation, so that if recognition becomes able to span (at least vegetative) generations in the recognizing plant as well as in the plant which is being recognized, then a consequence is that it becomes possible to reduce w by acting to exclude young 'alien' plants and favour the offspring of 'familiar' plants, attempting thus to attain a higher proportion of neighbours which, if not actually themselves familiar, are at least likely to behave like previously familiar plants.

Chapter 18. Two pot experiments

Gliddon and Trathan's (1985) experiment shows that the young vegetative propagules of a plant are able to benefit from the parent's *having grown beside particular plants* of another species - and that the effect is independent of any abiotic site influences. That of Grime *et al.* (1987) shows that the presence of VAM fungi enables (gross) direct transfer of assimilate from canopy dominants to subordinate plants; and that this is associated with substantially decreased growth of the dominants and substantially increased growth of the subordinates. Both of these experiments' results are consistent with the cooperation hypothesis which I have presented here, and neither has, I think, been satisfactorily explained in any other way. A more definitive test is, however, required. In this chapter, I describe a pair of experiments designed to accomplish that.

The hypothesis *that* plants cooperate, as I have presented it, gives rise to a series of hypotheses about *how* plants cooperate, which could be seen as (conjectural) stages in the evolution of cooperation.

It was necessary to decide *which* of these stages to test. The choice presented little difficulty in view of Gliddon and Trathan's results, since these suggest that *T. repens* and *L. perenne* have reached the stage of being able to recognize, and play against, particular individuals and their vegetative offspring.

The full hypothesis is thus that a non-ruderal plant is able to cooperate with a neighbour by giving and receiving resources via a VAM fungus. Such a strategy can only be evolutionarily stable on the basis of a relationship with a particular partner which reciprocates, and this relationship must require time to develop. Each partner must be able to recognize the other, and must also be capable of metering the amounts or value of resource given to and received from the other.

A pair of experiments were designed to test part of this. The first experiment was intended to show whether the effect of an apparent advantage due to familiarity, observed by Gliddon and Trathan (1985), is associated with an increase in direct carbon transfers.

The purpose of the second experiment was to test whether the length of time needed for a 'familiarity effect' to develop is too short for microevolution to be able to supply a plausible explanation.

The experimental design had to be such that a contrast exists between one pair of neighbouring plants which have been neighbours for a longer time and another pair which have been neighbours for a shorter time. Each plant must have been subject to otherwise identical treatment. In particular, if plants are planted or transplanted this needs to be done simultaneously to them all.

The desired contrast was accomplished by a 'familiarization' pretreatment in which plants grew in separated groups of neighbours, after which all were transplanted into new groupings in four inch pots. In such a new grouping, a plant is described as 'familiar' to another plant in the pot if the pair of them were neighbours during the pretreatment; or 'alien' if they were not. The essential difference between the two experiments was in the length of time over which familiarisation took place.

A decision was required whether:

- a) to contrast a treatment in which all plants were familiar versus another treatment in which all were alien to each other; or
- b) to contrast a treatment in which all plants were familiar versus another treatment in which all plants except one, alien plant were familiar.

The second of these approaches was taken on the grounds that if a donor plant which has the capability of cooperation has only alien neighbours it seems possible that it might be, as it were, forced into trying to develop cooperative relationships with them; whereas a donor plant having both alien and familiar neighbours seems likely to trade resources preferentially with the latter instead of the alien neighbour. In the new grouping (i.e. after the pretreatment), therefore, either all the members or else all the members except one are drawn from the same pretreatment group.

18.1. Choice of species:

One species only could be employed as the test plant, insufficient resources being available to evaluate both. In every case the single, alien plant in a new group was *T. repens*. This choice was made because *T. repens* is a 'guerilla' species (Gliddon and Trathan, 1985) it must, in the natural course of things, need to adapt/adjust to 'fit' previously unfamiliar neighbours more often than would be the case for *L. perenne* (a 'phalanx' species). I.e. the experimental set-up mimics a situation which is to some extent natural for *T. repens*, but would not be for *L. perenne*.

The two experiments differed in the form of familiarization pretreatment. In the first this occurred in the field. Plants were *found* growing in groups between 24th and 25th July 1989, and planted into treatments on the 26th and 27th July. Here, plants growing within 2 cm of each other when in the field were considered to be familiar, while plants growing at least 40 m apart, and separated by three or more riggs (i.e. ridges) and furrows, were considered alien.

In the second experiment the pretreatment group consisted of six plants grown together in a pot from seed for six weeks from 20th and 21st July 1989 until putting into treatments

on the 31st August and 1st Sept. Plants taken from the same pretreatment pot were termed familiar (to each other); those from different pots alien.

18.2. Materials and methods

The plant species chosen for both experiments were *Trifolium repens* and *Lolium perenne*, because these were the species found by Gliddon and Trathan (1985) to exhibit neighbour-related survivorship and growth⁴⁹.

18.3. Experiment I

Plants used in the first experiment were taken from an old meadow, in the belief that their ecological strategic character would thus be likely to be more stress-tolerant than that of plants from improved pasture (see next chapter for reasons why cooperative behaviour might be expected more from plants in poor habitats). Gliddon and Trathan's plants were also in old pasture.

The meadow, near Toddington, Bedfordshire, grid reference SP555243, occupies about 4 ha. parallel to the A5 road bounded to the southeast by the Ousel Brook, and to the north by a bridle path leading to Silsworth. It was surveyed in 1984 by Dr. Dony, County Botanist for Bedfordshire, and plants were taken by the kind permission of Mr. Roger Costin, the tenant.

18.3.1. Familiarization pretreatment

An attempt was made to choose the locations from which to take plants by random numbers; but this was abandoned when, after an hour of searching random locations, none were found in which *T. repens* and *L. perenne* were neighbours. Instead, four riggs were chosen randomly but with the criterion that none should be adjacent. Suitable locations were found by walking along each designated rig in turn, and pieces of turf containing both species were removed from them, and kept temporarily in labelled pots. Their location in the field was recorded, and they were brought back to the laboratory for transplantation.

18.3.2. Transplantation

During transplantation, roots were washed free of soil to eliminate, as far as possible, any site-specific effects. After weighing, plants were dibbled into pots already containing soil material. This was unsterilised loamy sand topsoil, from a different location than the plant material, which was air-dried, homogenised and sieved through a 0.5 cm mesh, then wetted up and allowed to equilibrate for four days.

⁴⁹ Even so, too much importance should probably not be attached to species as a determining factor of the degree of cooperative behaviour to be expected from a plant, since ecological strategy varies, often greatly, within species (Grime et al., 1988 passim).

Two *L. perenne* and one *T. repens* plants were arranged in an equilateral triangle in each pot. In half of the pots all three plants were familiar; whilst in the rest the two *L. perenne* plants were familiar with each other but alien to the *T. repens* plant. The choice of which plants to put together into treatment groups was made by the use of random numbers.

A replicate consisted of two pots: in one the *T. repens* plant had previously been a neighbour of the two *L. perenne*; whilst in the other it had not.

After transplantation was complete, the pots were mulched with clay balls to reduce water loss and weed growth. Treatment pot locations were randomized at start, and again half way through their growth, and were kept in the open at the East Gate field site of the Open University at Walton Hall, Milton Keynes.

18.3.3. Carbon transfer determinations and harvest

All the plants of both experiments were taken to Rothamsted experimental station on 25th October and the ^{14}C feeding and harvest was carried out on 27th October for experiment 1 and 6th November for experiment 2.

$^{14}\text{CO}_2$ was generated by adding 0.5 mCi of labelled sodium carbonate solution to a 250 ml conical flask in which 4.5 ml of 0.01 M unlabelled sodium carbonate had previously been placed. The unlabelled sodium carbonate served a dual purpose: ensuring alkaline conditions to prevent premature $^{14}\text{CO}_2$ production and also to give a total CO_2 concentration of about 2000 ppm in the gas mixture⁵⁰ fed to plants. The flask was then sealed with a 'subaseal' stopper, and one ml (i.e. excess) of 17M orthophosphoric acid was injected through the stopper using a hypodermic syringe.

The flask had a side arm to which a flexible gas reservoir had been attached, made out of a tough, polyethylene incontinence bag⁵¹. After the labelled gas had been generated it was diluted by injecting 350 ml of air through the stopper into the flask using a 50 ml syringe. The diluted labelled gas was homogenised by repeatedly withdrawing and re-injecting it using the same syringe, each time working the gas reservoir so as to re-mix its contents. The purpose of the flexible reservoir was to enable successive gas samples to be withdrawn at the same pressure.

In each pot, a donor plant of one or other species was nominated (using random numbers to decide which of the two plants to use if *L. perenne*) and the youngest fully expanded leaf chosen for $^{14}\text{CO}_2$ feeding. A self-sealing polythene bag was sealed to

⁵⁰ My thanks to Martin Cornelius of Rothamsted, who, in addition to much other help, recommended using such a CO_2 concentration.

enclose the leaf to be fed, the petiole being first sandwiched between two pieces of BICC Pyrotenax plastic seal compound. 10 ml of $^{14}\text{CO}_2$ was withdrawn from the flask by syringe and injected into the polythene bag, the puncture being immediately sealed with sticky tape⁵². The plants were left in the sun from about 10 am to 4 pm, when their roots and shoots were harvested. These were washed, weighed before and after oven drying, and then milled in a ball mill. Care was taken to handle first, from each pot, the material likely to be least radioactive (i.e. receiver shoots then roots, then donor roots, then shoots, then ^{14}C fed leaf) and hands were washed between pots, to minimize contamination.

Sub samples of approximately 50 mg taken from the milled material were weighed into counting vials. 1 ml of a tissue solubiliser ('Soluene 350', supplied by Packard) was added to each vial and left at 30 Celsius for 12 hours. 9 ml of scintillant ('Ultima Gold', also supplied by Packard) was then added and mixed, and the vials loaded onto an automatic scintillation counter. Results were printed out in counts per minute (CPM).

18.3.4. Results of the field-familiarized experiment

As an index of the degree of (gross) carbon transfer from donor to receiver plants, the Root Radioactivity Ratio was calculated. Root Radioactivity Ratio is the ratio of radioactivity in the donor's root to radioactivity in the receiver's root (CPM per g dry weight of the counted subsample).

The reasons for choosing roots rather than shoots were that it is from the root of the donor to the root of the receiver that any carbon transfer must occur, and some possible extraneous sources of variation may thus be excluded - for example those due to differences between the root-shoot import/export relations *within* different, receiver or donor, plants. In the donor, radioactivity was also expected to be more evenly distributed in the root than the shoot.

An ANOVA analysis was performed on the Root Radioactivity Ratios, using two independent variables - treatment and species of donor plant. The classical experimental approach was taken in which effects are assessed in the order factors first, followed by interactions. This analysis was not performed on all the results. Examination of the raw data of CPM shows that not all attempts at feeding $^{14}\text{CO}_2$ to 'donor' plants had succeeded: in some cases donor roots were not much more radioactive than receiver roots. For this

⁵¹ Stock No. 635 from Seton Products, Oldham.

⁵² I am indebted to Clive Powell, Institute of Grassland Animal Production, Hurley for suggesting this method.

reason results where the radioactivity of donor root was less than 30,000 CPM per g Dry Wt. were excluded (treated as missing values).

Neither treatment nor species had significant effect (P was 0.577 for treatment and 0.912 for species of donor). However the two-way interaction of treatment with donor's species was significant (P = 0.010).

Table 10. Donor/Receiver Root Radioactivity Ratios: A) Means and B) ANOVA

A) Means

TREATMENT	SPECIES OF DONOR	
	<i>Lolium perenne</i>	<i>Trifolium repens</i>
Alien	13.9652 (9.6043) n = 5	5.0292 (2.2626) n = 9
Familiar	4.5335 (3.2076) n = 5	12.4878 (10.7566) n = 10

B) ANOVA of C¹⁴ Ratio Donor/Receiver (CPM per g DW root counted)
BY treatment and donor species

Source of Variation	Sum of Squares	DF	Mean Square	F	Signif of F
Main Effects	19.649	2	9.825	.165	.849
TREAT	19.080	1	19.080	.320	.577
SPDON	.745	1	.745	.012	.912
2-way Interactions	466.821	1	466.821	7.820	.010
TREAT SPDON	466.821	1	466.821	7.820	.010
Explained	486.470	3	162.157	2.716	.066
Residual	1492.425	25	59.697		
Total	1978.895	28	70.675		

Values in brackets are standard deviations. Radioactivity measured as CPM per g D.Wt.

In the familiar treatment gross carbon transfer from *L. perenne* to *T. repens* appeared greater, whilst that in the opposite direction, *T. repens* to *L. perenne*, appeared smaller than was the case in the alien treatment. This result suggests that the effect of the familiarity

pretreatment was to promote *net* carbon transfer from *L. perenne* to *T. repens* plants at the time when the determinations were made.

Mean shoot dry weights follow only very weakly the pattern which might be expected from this apparent direction of net transfer - viz. that in the familiar treatment *L. perenne* shoots weigh less, and *T. repens* shoots more, than in the alien treatment. According to ANOVA analysis these differences are not significant.

These results support the hypothesis that the amount of carbon transferred between *L. perenne* and *T. repens* plants is affected by their *familiarity* with each other. The effect observed by Gliddon and Trathan (1985) - whereby plants derive apparent advantage in growth or survivorship from previous familiarity with their current neighbours - is associated with a difference in 'direct' nutrient transfer occurring between previously 'familiar' plants as compared to that between previously 'unfamiliar' plants. They also support the hypothesis that *net* 'direct' transfers of carbon are involved in this process.

Table 11. Shoot Dry Weight Means /g

TREATMENT	SPECIES	
	<i>Lolium perenne</i>	<i>Trifolium repens</i>
Alien	.359 (.202) n = 32	2.728 (1.206) n = 16
Familiar	.344 (.171) n = 32	3.065 (1.102) n = 16

18.4. Experiment II

The second experiment was similar to the first except for the following differences. Plants were grown together from seed in a familiarity pretreatment in four inch pots. They were arranged hexagonally around the pot with two *T. repens* seeds occupying opposing positions, and the other four vertices taken by *L. perenne* seeds. When transplanted into the final treatment pots, this arrangement was maintained. Roots were again washed, and five of each group of six were planted into the same spatial configuration with respect to each

other as they had in the pretreatment group. The sixth plant, a *T. repens*, was taken from a different pretreatment pot, becoming the 'alien' in the group. The experimental contrast was thus accomplished *within* a pot in the second experiment, and had for this reason a somewhat different character. Here, the *L. perenne* plants are each offered a choice between an alien and a familiar *T. repens* partner with which to form mycorrhizal connections.

18.4.1. Results of the seed-grown experiment

Although there was a difference between the dry weights of alien and familiar *T. repens* plants (0.709 +/- 0.302 and 0.776 +/- 0.299 g respectively); this was not significant when subjected to ANOVA analysis. This result does not support the hypothesis that Familiarity advantage is able to develop between *T. repens* and *L. perenne* over a period as short as six weeks.

The results of radioactive counting were disappointing, indicating that ^{14}C had not been taken up to any significant degree. This was probably because the experiment took place too late in the year when the weather was too cold for photosynthesis. This is especially unfortunate in that the design of experiment 2 was expected to be an improvement on the first design in the sense that it should be sensitive enough to show up facultative specificity in the choice of partners with which to cooperate.

18.5. Discussion of problems

One difficulty in the design of the experiments was the fact that the hypothesis cannot be tested directly. It is necessary in effect to test two hypotheses at once; in that one must make a prediction not merely *that* plants often play cooperatively 'against' each other, but also *what* will be their particular plays in a given situation. A potential shortcoming of both the experiments was that direct transfer of labelled carbon could only be monitored over a period of a few hours; and nothing was done to try to ensure that these would be hours during which resource trading was particularly likely to occur. Another difficulty is that it was not possible to sterilize plant roots before transplantation, so a number of organisms from the original field site would have been imported into the treatment pots; and these might have affected the test plants in unknown ways.

Despite the failure of experiment 2, the idea of drawing the experimental contrast within a pot may be worth considering as a way to carry out further work in this field, since the cooperation hypothesis which I am advancing is about a phenomenon essentially facultative rather than obligate in nature.

Chapter 19. Conclusions and discussion

In this third part of my thesis I have argued three propositions:

19.1. First proposition

There is no logical paradox in postulating that a plant might compete yet also benefit by cooperating with the same neighbour⁵³, at the same time and over the same resource. This was demonstrated through a thought experiment.

19.2. Second proposition

There is a gap of understanding in the literature: *we lack an explanation* of the commonly accepted fact that plants and VAM fungi are able to cooperate with each other. *Mutual benefit from the association is an insufficient condition for cooperation to be evolutionarily stable*. The association must also confer more fitness than do 'scrounger' strategies which would otherwise displace it.

Strictly, this may be said with any certainty only of the evolutionary *beginnings* of the relationship between plants and VAM fungi. Successful cooperative relationships have a tendency to evolve into unions⁵⁴ wherein two separate (although interacting) control systems become one unified control system (although this may still be, to some extent, distributed).

⁵³ It may be an example of terminology obstructing thought (see appendix 2) that this simple fact has, up to now, escaped notice. 'Competition', after being used somewhat loosely for a time, was in some danger of being phased out altogether as a term. Grime (1973) pleaded for its retention, but with a precise definition whose import was, effectively, that if two plants draw a growth resource from the same pool, then they are said to be competing for it (Grime did *not* add any rider that the term should only apply in the case of resources which are limiting - *sensu* Liebig, 1840). By this definition nearly all neighbouring plants compete with each other whenever they are using resources - by the mere fact of having their roots in the same soil volumes, and their leaves in the same beams of sunlight.

There is actually *precisely* as much reason to suppose that two people in the same room cannot cooperate because of the unquestionable fact that they are competing (*sensu* Grime) for oxygen as there is to suppose that two plants cannot cooperate while competing. I suspect that the reason that no-one appears to have thought of this before may be because the heavy load of associations which are carried by the word 'compete' overrode its explicit definition. I believe the necessity for a concept corresponding to Grime's definition of competition to be fundamental. Neither would I argue for a change of term. Yet had some other term been used, then perhaps it would not have stood in the way of the idea that plants may, like animals, be capable of cooperation.

⁵⁴ As mitochondria and chloroplasts have done, for example. In such a union the vehicle (*sensu* Dawkins, 1989) is what becomes single. Separate genetic systems persist as replicators, although these may be functionally completely dependent on each other.

Has this happened in the case of the VAM fungus-plant symbiosis? The fact that VAM fungi are unable to live without plants might suggest that it has, although their apparent lack of host specificity⁵⁵ could weigh on the other side. One approach to answering this question would be to apply Dawkins' (1989, page 243) criterion to the fungus: 'Are [the parasite's] genes transmitted to future generations via the same vehicles as the host's genes? If they are not, I would expect it to damage the host, in one way or another. But if they are, the parasite will do all that it can to help the host, not only to survive but to reproduce. Over evolutionary time it will cease to be a parasite, will cooperate with the host, and may eventually merge into the host's tissues and become unrecognizable as a parasite at all.'

The answer is, on the face of it, *no*: fungus genes do not follow plant genes when these leave the plant by the route of sexual reproduction. But the picture is more complex than this, firstly because the fungus may reproduce vegetatively to follow the plant's vegetative reproduction - growing parallel to an extending root and reinfesting it at intervals. Secondly, I believe that Dawkins' criterion should be generalised a little: *if the parasite's offspring gain benefit from the survival of the host's offspring then cooperation is to be expected*. This condition is met in the case where both host and parasite genes are transmitted by a common vehicle; but it might also be met in other ways. Such another way would exist if a plant's (vegetative or sexual) offspring had the ability to repay (Tit for Tat) a fungus' offspring for cooperation received from the fungus.

19.3. Third proposition

For Prisoner's Dilemma type cooperation to be possible the same abilities are required of the parties whether these are a plant and (ancestral) fungus, or a plant and another plant via a fungus. A plant cooperating with its neighbour needs to have:

- i) ability to *recognise* a neighbour
- ii) ability to *measure input* of resource from that particular neighbour
- iii) ability to *measure output* of resource to that particular neighbour
- iv) ability to *process* the above information⁵⁶ to make *evaluations* of how good a partner a particular neighbour has shown itself to be

⁵⁵ 'Apparent' because although any VAM fungus strain may infect a host plant in the laboratory, it is possible that in the field - where several VAM fungus strains are presented to the host - specificity exists as a higher preference for one strain than another. This is testable.

⁵⁶ Following Axelrod and Hamilton (1981), this information processing would need to be no more complex than remembering each partner's last play. However I would suggest that in the real world a strategy as simple as (digital - 'Yes or No') Tit for Tat would be open to invasion by a strategy which might be termed 'driving a hard bargain'. This would consist of plays which are in the same direction as Tit for Tat

v) ability to *store* either the evaluations themselves or the information needed to make them

vi) ability to *execute* the decisions indicated by these evaluations

If these abilities were not possessed by 'cooperative' plant strategists then scrounger strategists could displace them. Even if these requirements are not still in place for modern plant-fungus cooperation because the plant-fungus has, eventually, come under unified control (see above), we may feel confident that they do operate in the case of plant-plant cooperation since plants are presumably autonomous of each others control.

19.4. Initial research required

Following this work it can no longer safely be assumed that plants do not cooperate. *Evidence* is now required.

My results suggest that previous familiarity with present neighbour plants may affect the magnitude of 'direct' nutrient transfers. Research is required to determine the time scale over which such 'familiarity' may be induced. In this connection Fitter (1989) proposed that P transfers from VAM fungi may only be needed by the plant when it is a seedling or at times of reproductive resource drain. *If* the same were true of 'direct' resource transfers from other plants via VAM fungi then two things would follow. First, there is more scope for cooperation between plants of different species than there is between plants of the same species since the latter will tend to need the same resources at the same point in the year. Secondly, successive plays in a Prisoner's Dilemma game could only occur at annual intervals, and a long time (sufficient for flowering to occur) might be required for the process of 'familiarisation' to take effect under the sort of experimental conditions presented to the plants in my second experiment. This is because they all began as seedlings at the same time, and would presumably therefore not be in a position to be able to donate resources to each other. Seedlings grown with more mature plants, by contrast, might be expected to be able to form cooperative relationships more quickly with them, since seedlings are less able to supply their own needs for phosphorus than are older plants.

However, even accepting Fitter's proposition; *once given* the existence of infrastructure for resource-trading *via* VAM fungi, it seems at least possible that more regular trading between plants could happen. I suggest this because it seems to me that the situation

plays would be (i.e. Cooperate for Cooperate; Defect for Defect) but would involve donating smaller amounts of resource than had been received. What I am really saying here is that a cooperative plant needs to be able to run some kind of cost benefit analysis on each neighbour's transactions - perhaps if plants really are able to cooperate in the way that I postulate, then although both parties may benefit, the one with the best ability to process information may benefit more.

obtaining between two connected plants may be considered closely analogous to that between two trading nations; and that therefore the post-mercantilist economists' theory of trade may be applied to it. The analogy is between:

- a) goods with their costs of industrial production, and
- b) captured resources with the costs incurred by a plant in capturing them.

Ignoring cost of transport, wherever the *relative cost ratio* of two resources differs between two fungus-connected plants, then trade should be expected to be mutually profitable⁵⁷.

Thus if major game plays occur with annual frequency at flowering, this may not preclude more frequent minor plays occurring - through which a cooperative relationship may be built with a neighbour plant on the basis of differences in which resource is limiting. However, the existence of such a cooperative relationship based on minor transfers might not be sufficient to bring about major cooperation at flowering time. If the amounts or, rather, the values of transfers are much greater for the 'major' game, then this should perhaps be considered to be the first play in a new game rather than a continuation of the minor game.

On the other hand laboratory studies of PD games with human subjects show that cooperation is facilitated if they are able to communicate with each other (Colman, 1982). Minor games might possibly fulfil such a function for plants.

⁵⁷ More strictly, trade should be profitable where there is a difference between the respective trading partners' relative cost ratio of two resources, and this difference outweighs the marginal cost of transporting the two nutrients. The marginal cost of transport may be equated to the maintenance cost of arterial hyphae and any necessary associated structures. The important point about the theory of trade is that it can describe trade as rational for both parties even in a situation where one partner's costs of production are higher for both the resources being traded (the theory which this superseded held that one side always loses by trade). In the case of a dominant and subordinate pair of plants under temperate conditions, probably the cost of photosynthate production is less for the dominant than for the subordinate since it will trap more sunlight per unit leaf area. Their relative cost ratios of (Photosynthate cost / Nitrogen cost), for example, would probably then differ. If the subordinate were more stress-tolerant than the dominant, then its cost of winning N or P might be less; in which case the relative cost ratios of the two plants would differ still more.

It is possible to imagine a similar situation where the root systems (including any symbionts) of two neighbour plants differ. For example if only one were able to penetrate a compacted soil layer and reach a water table; or if one has nitrogen-fixing nodules; or if one is more finely distributed through the soil and is hence able to win phosphorus more cheaply.

Further research could be carried out to choose between Gliddon and Trathan's (1985) hypothesis and the cooperation hypothesis. Two predictions do follow from the cooperation hypothesis and do not follow from their alternatives. These are:

- a) that their 'local specialisation' effect would not persist in the absence of mycorrhizae; and
- b) that the effect might be induced *equally* by exposure to another plant during a familiarisation pretreatment whether this were the sole neighbour or only one among several neighbours in the same pot.

19.5. Further research: functional

Should the cooperation hypothesis which I have presented here gain acceptance, then further questions arise to be answered. These are of two types: about the behavioural patterns occurring, and about the physical mechanisms supporting them.

Study of behavioural patterns might concentrate first on the characteristics of the information storage and processing functions:

19.5.1. Information storage

How long does a cooperative relationship take to form? Does the degree to which a plant will *risk* resources (by donating them to a partner which is not certain to reciprocate) deepen with the duration of the relationship? How many cooperative relationships with neighbours may one plant *maintain* simultaneously⁵⁸? And how many partners can a plant retain the ability to recognise? How long can it retain the information necessary for cooperation during vegetative growth? Does this information travel with growing vegetative parts or does it remain local to where it was first *learned*? Is it even able to pass through the stage of sexual reproduction? If so, then via pollen or ovum or both? Might it - still less plausibly - be passed on *symbolically*; i.e. *taught* to one plant by another? If so then this would have the advantage that it would cost the giver of information virtually nothing. Properly speaking, this would bring it outside the scope of Prisoner's Dilemma game theory.

19.5.2. Information processing

Does a cooperative relationship with one partner influence future behaviour towards close relatives of the partner? How important is the *mutuality* of information about past cooperations? I.e. what happens in the situation where plant A recognises plant B but plant B does not recognise plant A (as could happen if plant B were descended vegetatively from the same genome line as A's 'remembered' partner, but via a different branch)?

⁵⁸ Prediction: about six.

19.5.3. The experimental method

The same basic method can be used to draw all the experimental contrasts needed to answer the above questions. It consists of pretreatments which give the opportunity of familiarization to particular pairs of plants; followed by propagation or transplantation to form new groupings. Evaluation of any advantage due to familiarity may be accomplished by measuring labelled nutrient (or chemical analogue) transfer and/or effect on growth (as a surrogate for fitness).

19.5.4. Predictions

A note of caution: we probably need to be monitoring *resources which are in minimum*, rather than others. Further, if the cooperation hypothesis is correct it will prove impossible to understand (for example) carbon transfers alone - they will only be explicable as one component in an integrated system involving any growth resources which are in short supply at any time in the life-cycle.

The cooperation hypothesis also suggests that transfers between neighbouring plants will turn out not to be explicable solely in terms of the physical basis of particular mechanisms of transfer - we will also need to understand net transfer patterns in terms of what is in the interests of the plant's survival and reproduction - i.e. fitness.

19.6. Further research: mechanism

What is the physical basis of the information-processing power and information storage capacity of plants? One possibility is the genome. This suggestion would have been fatally flawed, until recently, by the belief that the genome is subject to mutational change in the vegetative phase only very slowly, by radiation damage etc. It is now becoming accepted, however, that, '*somatic mutation*' occurs at a substantial rate (Antolin and Strobeck, 1985). Further, many genes are part of a cascading system of *switches* (so that a gene may carry *information* by the fact of being switched either on or off, without any mutation being involved). The task usually ascribed to this system is the overall control of cell development; but it may be that its capabilities are more general and more generally applied⁵⁹.

In this connection it is interesting that plants have such a strong tendency toward polyploidy, which is relatively rare in animals. Bennet (1987) remarked that the adaptive significance of the extra genetic material has not yet been found. It is at least possible that

⁵⁹ It is worth noting how similar the idea of chromosomes as information processing systems is to a Turing Machine - the archetype of a general purpose computer.

this exists in an increased capacity to handle information (*pace* Grime and Mowforth, 1982).

19.7. Economic implications of the hypothesis

Could a 'familiarity effect' be applied to increase the profitability or security of managed ecosystems? To answer this we would need to know more about it.

It is possible that it could be useful in agroforestry, where it might lead one *to propagate from existing parent material in a way that is spatially coherent*, reproducing the parents' spatial relationships by mapping them onto new ground being planted.

On the other hand it is also possible that if a plant with the ability to cooperate were 'thrown together' with unfamiliar neighbours (as must usually happen when plants are propagated by man) it is under evolutionary pressures to cooperate quickly anyhow. In this case, familiarity would only have an influence on its behaviour when it was grown with both familiar and unfamiliar neighbours at the same time, and would probably not be economically important.

If it *were* possible to increase yields or security to a useful extent, then how this might be accomplished would depend on the ways in which (or barriers across which) plants are able to retain the information necessary to cooperation. For example the effect might be usable via vegetative propagation methods; but not via seed.

19.8. What can the hypothesis explain?

As well as explaining why the VAM fungus-plant association persists, why familiarity was associated with increased growth or survivorship amongst the plants observed by Gliddon and Trathan (1985) and others and why arbuscular hyphae exist; the cooperation hypothesis could also help to explain an old conundrum: why is it so difficult for most aliens to invade strange plant communities? It seems at least possible that, in a community of long standing in which virtually all plants have had considerable opportunity to develop cooperative relationships with neighbours, an outsider would be at a serious disadvantage.

Would cooperation affect diversity? If cooperation confers significant advantage on the plants already in a locality, thus making invasion more difficult, then this may increase species diversity by slowing or preventing the replacement of existing populations by more efficient invaders.

Perhaps closely related to this point is the explanation offered by the cooperation hypothesis of the reason why plants of disturbed habitats are less mycorrhizal than others. Such a ruderal plant opportunistically exploits a patch of habitat during the (naturally brief) period after destruction of the previously existing biomass has rendered it suitable for the ruderal's occupation, and before it becomes too overgrown again. The offspring of ruderal

plants tend to establish far from the parent because such exploitable patches of habitat are few and far between. A ruderal genome line is therefore likely to lack the continuity of locality necessary to give a high value of w - probability of reencounter. Given a low value of w , it is less likely to be rational for a ruderal plant to practise cooperative behaviour than it is for other plants to do so.

Accepting the argument that cooperation is more possible between plants of different species (see above), could cooperation also help to explain the large yield advantages found in intercropping experiments (Willey, 1979a, 1979b)?

Another phenomenon which the cooperation hypothesis could explain is the persistence of juvenile trees in the understorey of a tropical rainforest despite extremely low incidences of photosynthetically active light. Here may be an ideal situation for cooperation to thrive since the trees of the upper canopy may have a much higher availability of light and a substantially lower availability of CO_2 than will understorey plants. Trading of CO_2 for photosynthate would, if it were possible, therefore be advantageous to both partners and could supply a rationale for the direct transfers from canopy dominants to subordinates which Grime *et al.* (1987) postulate.

19.9. Differences between computer simulation and real world conditions

Is simple Tit for Tat strategy optimal in the real world? One factor militating against this is that *the probability w of re-encounter* does not always remain constant: '[T]he ability to monitor cues for the likelihood of continued interaction is helpful as an indication of when reciprocal cooperation is or is not stable. In particular, when the value of w falls below [a certain] threshold [...] it will no longer pay to reciprocate the others cooperation. Illness in one partner leading to reduced viability would be one detectable sign of declining w . Both animals in a partnership would then be expected to become less cooperative. Aging of a partner would be very like disease in this respect, resulting in an incentive to defect so as to take a one-time gain when the probability of future interaction becomes small enough.'

The effect of this on game strategic interactions between long-lived interactants in an environment sometimes subject to severe stress seems likely to be that only to take account of the partners' previous play, as Tit for Tat strategy does, is suboptimal. If the partner becomes more likely to defect under stressful conditions (which may be precisely those under which defection of a partner is most damaging), then it may become important to base one's play on a strategy of preferring partners expected to be reliable when conditions get difficult.

A further point: there may be an additional dynamic, not treated by Axelrod and Hamilton (1981), which acts to favour cooperation. This is that in a highly stressful environment, where resources are only intermittently available, cooperation is rational because in it lies the *only* hope of survival. Such a motive may operate among poor human communities.

In the computer, plays are discrete and simultaneous, whereas in the real world plays may be alternate *or* continuous. Axelrod (1984, p.95) believes these differences unimportant: 'The [iterated Prisoner's Dilemma] model does assume that the choices are made simultaneously and with discrete time intervals. For most analytic purposes, this is equivalent to a continuous interaction over time, with the length of time between moves corresponding to the minimum time between a change in behaviour by one side and a response by the other. And while the model treats the choices as simultaneous, it would make little difference if they were treated as sequential.'

Two further complications have not been adequately dealt with in work on cooperation. The first is the possibility that a player might exercise *choice* of playing partners; although Axelrod and Dion (1988) review some work on *n*-player games in which *ostracism* - which is a limited form of choice of players - is allowed. It seems a reasonable presumption that introduction of the choosing of partners into the game would tend to favour cooperation.

The second is the possibility of analogue plays - i.e. what would happen to the conditions under which cooperation is viable if, instead of just the two (digital) options of Cooperate or Defect, any value within some range could be played⁶⁰? Axelrod (1984) makes the suggestion that one answer to the problem of two players who, although capable of mutual cooperation, become locked into a series of retaliatory defections would be to employ plays of 90% Defection, rather than full Defection. It is thus clear that he is aware that analogue plays would introduce new possibilities into the game; but what these might be remains unexamined. The question of analogue plays is important because so many real-life situations are better mapped by it than by digital plays. I conjecture that an important consequence of introducing analogue plays would be that successful strategies would need to be considerably more complex - i.e. strategists would require more intelligence.

19.10. Information-processing, learning and intelligence in plants

The ability of plants to process information, although rarely stated, cannot be doubted. It is seen wherever environmental cues trigger *appropriate* behaviour, beginning with the downward-growing response of the germinating radicle to gravity. It may be viewed as

representing the fruits of *learning* by the genome line. This is, after all, merely a way of describing any evolution of increased fitness.

Does the genome line produce plant 'individuals' able themselves to learn? In this work I have argued that - in order to cooperate - plant individuals must be able to learn. Are plants intelligent? Good definitions of intelligence are hard to come by; and it may be easier to talk instead of *learning capacity*, as I have done here. However the (tacit) convention that intelligence may be ascribed to animals (e.g. Rozin, 1976); but never to plants deserves to be questioned. There are only three alternatives. These are firstly that plants have zero intelligence; or secondly that intelligence is an inappropriate term for their abilities to process information; or lastly that plants should be seen as intelligent. Whatever may be the answers to these questions, should not the criteria on which they are answered be the same for plants as for animals?

We do not yet know what is the ceiling of possible plant information-processing capacity or of learning ability/intelligence. We need to recognize that these questions exist and have importance.

⁶⁰ Such a game does not fall within the definition of Prisoner's Dilemma, which may make it less likely to be analysed.

Chapter 20. General Conclusion

This PhD thesis set out to contribute towards development of methods to improve our capability in the design of spatiotemporal planting patterns for Agroforestry production. Carried out in a Systems department, it began from a Systems viewpoint. Identifying as a key difficulty the colossal cybernetic variety of agroforests (i.e. the number of possible different agroforests which could exist), and assuming that a major factor of that variety is generated by the many possible interactions between neighbouring plants, I decided to make such interactions my thesis subject.

Three approaches were made to the problem, which correspond to the three part division of the thesis. In each of these I looked among the ideas and methods of wild Plant Ecology, seeking to bring back each time something potentially useful to the managed ecosystems of Agroforestry.

Part I attempted to apply insights from theory on the ecological strategies of wild plants to make a specific contribution towards a typology of agroforests in terms of the C-S-R model. From this theory came a hypothesis that an 'S' type overstorey would be likely to interfere less than would a 'C' type overstorey with an understorey crop through its root system's pattern of spatial occupation. An experiment contrasting Holly with a Poplar as overstorey plants yielded results consistent with the prediction. However, the question remains: how applicable is C-S-R theory to artificially selected plants? (that is, How far does an ecological strategy cohere after the natural selection processes which maintain it are replaced by artificial selection?); and many more results from similar experiments on different species would be needed before this hypothesis could become a useful rule of thumb for agroforesters.

Part II sought to contribute towards the harnessing and adaptation of neighbourhood spatiotemporal dynamic models, developed by plant ecologists, for quantitatively evaluating and optimising agroforest designs. In 1988, when this work was done, multispecies situations were considered complex and difficult and were not, in general, modelled; but agroforests are multispecies systems.

Growing five garden 'annuals' and a weed as model trees to yield some data to work with, and borrowing an idea from the solution of a formally similar problem in the evaluation of malnutrition in human populations, I found that using z-scores instead of raw parameters seems to allow a working multispecies distance model to be nearly as simple as a single species one, and enables performance indices of different species to be aggregated as desired and related to neighbourhood spatial parameters.

Individual-based distance models were developed mainly for scientific reasons; but their application to cropping systems will of course be for economic purposes, and I indicate how this might plausibly be accomplished. First, by running 'backwards' the regression equations relating performance of each component species to neighbourhood predictor variables, we can obtain a predicted yield for each component of a given planting pattern. Second, this can be expressed as a predicted LER for each component, summing to a predicted LER for the agroforest design, which enables easy economic comparisons of different designs. Third, the capability to do this, provided it be not too computationally intensive, could be used (as the evaluation subsystem) without too much difficulty by a 'genetic algorithm' program to (literally) evolve designs which optimise the positive and negative interactions between neighbour plants to give an (approximately) maximally productive design.

Whereas Parts I and II owed much to ideas in Plant Ecology which were, though youthful, already quite successful, Part III tackled a problem for which no ready made theory was available. This began from a realisation that the recently discovered existence of 'direct' nutrient transfers between plant neighbours, because they appeared to greatly affect the growth performance of wild plants, were highly likely to have substantial implications also for Agroforestry design, which had been neither considered nor guessed at.

The discovery of direct nutrient transfers did not seem to have plausible explanations within the almost universally accepted competition paradigm of plant ecology: when two plants grow close enough to interact with each other they are competing for resources; therefore they cannot cooperate. Reading between the lines of the *direct nutrient transfers* debate, it seemed both proponents (Grime *et al.*, 1987) and opponents (Newman, 1988) realised that cooperation between plants would have to be seriously considered if direct nutrient transfers turned out to be a reality.

A break through this logjam was supplied by a thought experiment whose result was the finding that competition and cooperation between two organisms can, in principle, take place at the same time and over the same resource, in the sense that both organisms may benefit from cooperating despite simultaneous competition. Although the finding may have interest in its own right, it bears one implication which is of particular interest for my thesis, which is that it removes one of the two possible reasons why plants could be thought unable to cooperate. Before this finding, it might have been thought that a hypothetical plant with a mutant *physical* ability to cooperate would lose fitness by making use of that ability. Now, it should be seen that if this mutant plant is assumed to possess the

necessary physical wherewithal to cooperate, it *would* be in its survival or reproductive interest to do so.

This finding enabled a theoretical investigation of what, precisely, would constitute for a plant the 'physical wherewithal to cooperate'. Based on the Iterated Prisoner's Dilemma paradigm, the investigation brought together findings and, especially, what I suggest may be seen as core problems from the two fields of *biotic specialisation* and *direct nutrient transfers*. In a nutshell these are the questions 'Why do canopy dominants transfer nutrients to their subordinate neighbours?', and 'Why does previous familiarity between *L. perenne* and *T. repens* individuals lead to decreased growth of *L. perenne* and increased growth of *T. repens*?' I have argued that it would be a single solution to all these problems to hypothesize that plants may practice a form of IPD cooperation with each other⁶¹.

The capabilities which would be needed to underpin inter-plant cooperation were found to be considerable and exacting; but, despite this, in each case the possibility that they may have evolved found some evidence in its favour and could not be ruled out. The argument here followed the course of a hypothetical evolutionary pathway along which cooperation could have developed, in which each step is relatively small and also plausibly more beneficial than the previous step.

A simple pot experiment was planned and carried out to test the effect of their familiarity with each other on direct nutrient transfers between neighbour plants. The prediction that more carbon would be transferred between familiar neighbours was borne out in the case of plants whose familiarity was induced in the field. Although much more work will be necessary to confirm this finding, since its acceptance would represent a major shift, it is no longer safe to *assume* as axiomatic that plants do not cooperate with each other. Following this work, that conception should be demoted to the status of a testable hypothesis.

⁶¹ If, on the other hand, this hypothesis cannot be countenanced, it may yet be more useful to think about the two problems together than apart, since they have, at least, too much in common to merit their continued isolation from each other.

APPENDICES

Appendix 1. The Status of the Model

I explained, in Part I, Grime's original thesis, and some of what I consider to be its implications for those concerned with biological aspects of Agroforestry. If his model is correct it is clearly important for both pure and applied Plant Ecology. What is its status, in the sense of its perceived validity and importance?

It would be quite misleading to deal with this topic based only on published texts; since what scientists *say* about Grime's model is also important. There is a climate of conflict beleaguering ecological strategy ideas which seems to be specific to plant (as opposed to animal) studies. When I first drafted the kernel of my thesis on ecological strategies and Agroforestry I asked for comments and got a double-humped distribution of positive and negative responses. The negative ones were all by plant biologists and were often initially expressed forcefully. When pressed these always stated early that to apply the word 'strategy' to plants is invalid because it implies consciousness on their part; whereas plants cannot have consciousness; but none would engage in much debate.

I felt I was dealing with a wraith which I became very concerned to try to get to grips with. It was not easy to track down a *published* attack, and when I eventually did (Harper, 1982) it, too, seemed rather wraith-like:

Harper's treatment of Grime

Harper (1982) devotes his central thrust to an attack on Grime; yet never cites or mentions him. It is a little difficult to criticize him, because it is hard to get hold of his conclusions. Rather than stating, he leads us to infer them and often covers himself further by explicitly contradicting them later. He makes three suggestions:

a) Natural selection is only one of many causes of evolution.

It is only '*perhaps*' the most important - other factors (which he lists at length) may have caused any particular piece of evolution observed. That we cannot safely use the existence of natural selection in any particular case as a working assumption is presumably what we are being led to conclude:

'yet post-Darwinian Victorian optimism continues in much ecological thinking - that the organism should and can be interpreted as a perfected product of an all-embracing, idealizing and optimizing process of natural selection.'

Furthermore 'adaptation' is a hypothesis which has been set up in such a way that any observation must confirm it - i.e. it is not disprovable. Therefore, presumably, it does not conform to the accepted Popperian criterion of scientific method:

'If all the plants in a waterlogged habitat contain aerenchyma this can be seen (and taught!) as a splendid example of convergent evolution; if some have aerenchyma, some have superficial roots, others have mechanisms that prevent the formation of toxic anaerobic byproducts and yet others are able to metabolize such products, we have a splendid example of evolutionary divergence [...]. There are no losers in this type of investigation'.

What is wrong with this analysis is that not *all* observed similarities or differences *are* taken as examples of evolutionary convergence or divergence; but (usually and defensibly) only those in which the researcher thinks she or he can see some way in which the character concerned increases survival and reproduction chances⁶². An adaptation hypothesis *can* be disproved: if one finds a plant with characters which appear to militate against survival and reproduction in a habitat where it is found, then it is *not* adapted to that habitat; and it is not difficult to find examples of this where a plant is growing at the margins of its environmental range; and again Harper lets us know, later in the paper, that he is aware of this situation's existence. Why then has he not made the connection?

'There is every reason to suppose that most aspects of the form and behaviour of an organism represent the result of some set of compromises. Thus it is *dangerous* to search for interpretations of any isolated part of the form or behaviour of an organism and to give it an explanation in its own right as an optimal system.' (my emphasis)

What is going on here? On the face of it, Harper is right in that one cannot assume that any (arbitrarily?) 'isolated part' is a viable system; but does anyone actually do this in ecology? I cannot think of examples. On the other hand, the clause that 'it is dangerous to search for interpretations of any isolated part of the form or behaviour of an organism', *if he means it to stand independently of the rest of the sentence* is important, wrong, and damaging to scientific enquiry. But, once again, he is protected against challenge by not being clear.

'[R]ather than concentrating on a search for the ways in which organisms are perfectly suited to their environments, we might more *healthily* concentrate on the nature of the limitations that constrain where they live.' [my emphasis]

⁶² and Harper demonstrates that he knows this when he gives definitions of 'adaptation' later in the text.

Again, not a flat enough statement that one can contradict it flatly; but he is very wrong if he means us not to try to understand ways in which plants are suited to their environments - especially from the point of view of ecological production management.

b) Intra-species variation is so wide that generalization is inadmissible at the species level.

This, though too extreme to be credible, may have been a useful implicit criticism of Grime's practice of characterizing plants' strategies at the species level; since it may have been the reason Grime (1984) and Grime *et al.* (1988) subsequently mapped some intra-specific variations in his triangular nomogram with isopleth lines, instead of the previous representations by single points. This is a step forward: intra-specific variation is important and can be dealt with in Grime's paradigm. Indeed it must be - we cannot rely on strategy characterized in particular populations to represent the whole species. This does not render the approach useless for the plant breeder; but rather careful work will be needed on choosing individual plants - especially trees - from the wild or from indigenous cropping systems to use in Agroforestry systems

c) 'Adaptation' and 'strategy' are teleological concepts, etymologically implying goals, and therefore cannot be applied to plants.

This is the charge against Grime that seems actually important in preventing scientists from using his ideas (judging by what they say). *Yet again, Harper's words are equivocal:*

'[The distinction...] between the behaviour of the organism as explained in terms of its present properties (proximal explanation) and the explanation of how it comes to possess such properties, i.e. the evolutionary forces that acted on the populations from which the organism's ancestors were drawn (ultimate explanation) [...] becomes especially confused in the now common use of the word "strategy" to describe the programmed biology, especially the life-cycle, of an organism. The term "strategy" sounds like a teleology - as if the organism has a planned campaign of behaviour aimed at the future. Ghiselin (1974) justifies the use of the word and puts it into terms appropriate for ultimate explanation: a strategy "somewhat resembles the proverbial military school which produces officers admirably equipped to fight the battles of previous wars", i.e. a strategy is a property that is by, with or from the past. In most writing by ecologists, however, "strategy" seems to imply a plan for future survival - a programme designed to achieve a goal.'

From the point of view of scientific validity this attack is easily disposed of: Harper is ignoring Grime's *definition* of 'strategy'. He therefore presents no challenge to the concept,

and the best result he can permissibly hope for is to force a mere change in the term used for 'strategy'⁶³. Nevertheless it is scientists' *perceptions* of validity which direct the development of Science, and Harper's perception of plant strategy as an invalid concept is shared by too many to let the matter rest there. One of the most striking gaps in the literature documenting our discovery of the physiological functioning of plant roots, for example, is the lack of the idea that any of the (as they then seemed) extraordinary things that plant roots were discovered to be able to do might profitably be investigated from the point of view 'what would it be to the advantage of the plant's survival to do?'. Time and again papers put forward possible reasons for observed behaviour without including the reason of it's being simply *advantageous*; and this attitude, to the extent it informed thinking as well as writing, must have been a powerful brake on the *formulation* of hypotheses along the lines of 'The ability to do such and such would be advantageous to some plants: let's test if they can.'

What is needed is not merely such an easy defence of the concept of strategy as that *it* has not been attacked in the literature; but a more positive statement which results in scientists being able to think comfortably of plants as likely to exhibit characters which enhance survival chances.

One starting point here could be Structuralism's tenet that it is scientifically valid and useful to show how some observed structure is helpful to the entity in which it has been observed, even if one can say nothing about how it came into being. It was proposed originally by the anthropologist Levi-Strauss in his study of the complex rules governing endogamous and exogamous marriage amongst Australian Aborigines. He was able to show that the rules resulted in stability for the size of kinship groups; but not how they arose. Were they consciously designed? Or were they the result of natural selection operating against tribes with (functionally) less effective marriage rules? Such hypotheses were probably untestable, and without his modification of the then existing scientific method, Levi-Strauss would not have been able to publish his findings.

Thus, to return to plants, we could get used to seeing validity in understanding how particular behaviours/structures are helpful to plants without necessarily being able to suggest how they came about. But we should be able to do better than this.

⁶³ Harper also attacks the use of 'stress' on similarly purely etymological grounds.

Appendix 2. Terminology for thinking about plant strategy and adaptation

There is, I believe, a general problem of language in dealing with evolutionary adaptations of plants. This arises in part from the difficulty that it is usually impractical to measure an increase in *fitness* due to some character or treatment. Instead, one may have measurements of increase in biomass, for example. Harley (1989) cautions that one should therefore not talk of the 'benefit' of such a factor. Harley is right here in the sense that statistically valid proof of an increase in growth is not proof of increased fitness. Yet variations in fitness are the very engine of evolution, and if it is impermissible to speak of fitness we cripple our ability to understand evolution's products.

If some natural and widespread factor such as mycorrhizal infection confers on a plant an increased ability to grow, then, unless evidence exists to the contrary, it must surely be considered *most likely* that the plant is also fitter for it; the more so when, as is often the case, mycorrhizal symbioses appear to be obligate on the part of both symbionts. Whilst the statement 'mycorrhizal infection benefits X' may be epistemologically invalid, we need not, on that account, be dissuaded from such an alternative form as 'mycorrhizal infection *appears* to benefit X'.

Secondly, there is the seldom written (but commonly spoken) rule that one must avoid any form of words which might be construed as ascribing consciousness or will to a plant: 'Adaptation' and 'strategy' are teleological concepts, etymologically implying goals, and therefore cannot be applied to plants (Harper, 1982).

This has made many workers feel they must not use the simple everyday language of *decision* in speaking about plants; and the alternative, which is perceived as valid, is so unwieldy as to discourage use or understanding. One worker dealt with the problem as follows:

'May I [...] suggest that the reader not be dismayed by a terminology that might best be termed evolutionary shorthand. The statement "...it is likely that heavy investment in chemical protection of their few leaves is worthwhile," may be transliterated to read, "Those mutant genotypes that produce toxic foliage with resources that are used for other processes in the original genotype have a higher relative fitness in plants with small leaf crops than in those with large ones." ' (Janzen, 1975, page v)

Does such language need, though, to be justified as 'shorthand'? The crux of the matter seems to be that plants should be considered not to possess consciousness therefore we cannot speak of them as though their actions have *goals* (such as, implicitly, increasing

fitness in the example above). But the genotypic changes in a *genome descent line*⁶⁴ over evolutionary time are surely the output of a goal-seeking (and learning) system within a Systems definition. For example the Open Systems Group (1981, page 18) defines a goal-seeking system as 'a system that can respond differently to events until it produces a particular state (outcome).' That outcome being, in the present case, survival.

The 'pruning' of maladaptive evolutionary blind-alleys (by interaction with the environment) constitutes learning on the part of the genome line, whose goal we may define as its own continuation. Evolution is the learning process of a genome line. Provided we are clear that we are talking in terms of the genome line, rather than the individual (through which its decisions are expressed) it should therefore be permissible to use the language of decision and of teleology⁶⁵.

A result of these difficulties has been that workers in the field of plant ecology are shy of dealing with questions as to *why* plants do things, tending, rather, to confine themselves to questions of *how*, in terms of physical mechanisms. In this work, although discussion of mechanism is also important, I am dealing first and foremost with questions of *why* plants do things, and have tried to employ language that is simple and comprehensible. I beg the reader who finds this unacceptable to try to separate semantic disagreements from (other) matters of substance.

⁶⁴ *Line* is, perhaps, rather a poor term for the network structure of strands forking every generation and anastomosing every sexual generation.

⁶⁵ defined as the 'view that developments are due to purpose or design that is served by them' (OED).

Appendix 3. Programs and Data

Part 1 Programs

{programme uses raw data file to create 1 or 2 matrices}
PROGRAM matriculate (input, output);

LABEL 999;

CONST

 x_max = 17;
 y_max = 21;

TYPE

 file_name = varying [80] of char;
 param_record =
 RECORD
 species_a : integer;
 species_b : integer;
 scale_factor : integer; {COULD TRY A REAL HERE}
 END;
 data_record =
 RECORD
 date : integer;
 treatment : integer;
 block : integer;
 window : integer;
 x_real : real;
 y_real : real;
 species : integer;
 END;

VAR

 data_rec : data_record;
 exception_rec : data_record;
 param_rec : param_record;
 input_data_file : text;
 parameter_file : text;
 exception_file : text;
 output_matrix_file_a : text;
 output_matrix_file_b : text;
 sub_y : integer;
 sub_x : integer;
 successful : boolean;
 x_transformed : integer;
 y_transformed : integer;
 matrix_a : array [0..y_max, 0..x_max] of integer;
 matrix_b : array [0..y_max, 0..x_max] of integer;

PROCEDURE open_input_data_file;

begin

 open (file_variable := input_data_file, {internal name}
 file_name := 'raw_data.dat', {external name}
 default := '[c_eve.exptl.intermedata.roots]',
 history := old,
 error := continue);

 if status (input_data_file) > 0 then

```

        begin
            writeln(output, 'input data file error status: ',
                status(input_data_file));
            goto 999;
        end;
        reset (input_data_file);
    end;
PROCEDURE open_parameter_file;
begin
    open (file_variable := parameter_file, {internal name}
        file_name      := 'parameters.dat', {external name}
        default        := '[c_eve.exptl.intermedata.roots]',
        history         := old,
        error           := continue);

    if status (parameter_file) > 0 then
        begin
            writeln(output, 'parameter file error status: ',
                status(parameter_file));
            goto 999;
        end;
        reset (parameter_file);
    end;
PROCEDURE initialize_matrix; {(VAR param_rec : RECORD)}
{initialize with zeros}

BEGIN
    sub_x := 0;
    while sub_x < x_max do
        begin
            sub_y := 0;
            while sub_y < y_max do
                begin
                    matrix_a[sub_y, sub_x] := 0;
                    if param_rec.species_b <> 0 then
                        matrix_b[sub_y, sub_x] := 0;
                    sub_y := sub_y + 1;
                end;
            sub_x := sub_x + 1
        end;
    END;
PROCEDURE get_next_rec;
{read line of input file}
begin
    readln (input_data_file, data_rec.date,
        data_rec.treatment,
        data_rec.block,
        data_rec.window,
        data_rec.x_real,
        data_rec.y_real,
        data_rec.species);

    end;
PROCEDURE transform_data_point;
{divide intersect coords by scale_factor then truncate them}
begin
    {needs the scale factor putting in}
    x_transformed := trunc(data_rec.x_real);
    y_transformed := -1*trunc(data_rec.y_real);
end;
PROCEDURE add_to_matrix_a;

```

```

begin
  matrix_a[y_transformed, x_transformed] :=
    matrix_a[y_transformed, x_transformed] + 1;
end;
PROCEDURE add_to_matrix_b;
begin
  matrix_b[y_transformed, x_transformed] :=
    matrix_b[y_transformed, x_transformed] + 1;
end;
PROCEDURE open_exception_file;
begin
  open (file_variable := exception_file, {internal name}
        file_name      := 'matriculate_exceptions.dat',
{external name}
        default        := '[c_eve.exptl.intermedata.roots]',
        history         := new,
        error           := continue);

  if status (exception_file) > 0 then
    begin
      writeln(output, 'matric excepz file error status: ',
              status(exception_file));
      goto 999;
    end;
  rewrite (exception_file);

end;
PROCEDURE open_output_matrix_files;
begin
  open (file_variable := output_matrix_file_a, {internal
name}
        file_name      := 'mata.dat', {external name}
        default        := '[c_eve.exptl.intermedata.roots]',
        history         := new,
        error           := continue);

  if status (output_matrix_file_a) > 0 then
    begin
      writeln(output, 'output file A error status: ',
              status(output_matrix_file_a));
      goto 999;
    end;
  rewrite (output_matrix_file_a);

  open (file_variable := output_matrix_file_b, {internal
name}
        file_name      := 'matb.dat', {external name}
        default        := '[c_eve.exptl.intermedata.roots]',
        history         := new,
        error           := continue);

  if status (output_matrix_file_b) > 0 then
    begin
      writeln(output, 'output file B error status: ',
              status(output_matrix_file_b));
      goto 999;
    end;
  rewrite (output_matrix_file_b);

end;

```



```

PROCEDURE output_matrix_files;
begin
  open_output_matrix_files;
  for sub_y := 0 to y_max do begin
    for sub_x := 0 to x_max do begin
      write (output_matrix_file_a, matrix_a
[sub_y,sub_x]:2);
    end;
    writeln (output_matrix_file_a);
    end;
    for sub_y := 0 to y_max do begin
      for sub_x := 0 to x_max do begin
        write (output_matrix_file_b, matrix_b [sub_y,
sub_x]:2);
      end;
      writeln (output_matrix_file_b);
    end;
  end;
PROCEDURE test_data_point (var successful: boolean);
begin
  successful := true;
  if (x_transformed > x_max) or (y_transformed > y_max) or
    ((data_rec.species <> param_rec.species_a) and
    (data_rec.species <> param_rec.species_b)) then
    successful := false;
end;

PROCEDURE add_to_exception_file; {shove further up}
{write the raw_data.dat line to the exception file}
begin
  exception_rec.date := data_rec.date;
  exception_rec.treatment := data_rec.treatment;
  exception_rec.block := data_rec.block;
  exception_rec.window := data_rec.window;
  exception_rec.x_real := data_rec.x_real;
  exception_rec.y_real := data_rec.y_real;
  exception_rec.species := data_rec.species;

  writeln (exception_file,exception_rec.date,
          exception_rec.treatment,
          exception_rec.block,
          exception_rec.window,
          exception_rec.x_real:3:4,
          exception_rec.y_real:3:4,
          exception_rec.species);

end;
BEGIN {main prog}
  open_input_data_file;
  open_exception_file;
  open_parameter_file;
  read (parameter_file, param_rec.species_a,
        param_rec.species_b,
        param_rec.scale_factor);
  get_next_rec;
  initialize_matrix; {param_rec}
  while not eof(input_data_file) do
    begin
      transform_data_point;

```

```

        test_data_point (successful);
        if not successful then
            add_to_exception_file
        else
            begin
                if data_rec.species = param_rec.species_a then
                    add_to_matrix_a
                else {ie if data_rec.species =
param_rec.species_b}
                    add_to_matrix_b;
            end;
            get_next_rec;
        end;
        output_matrix_files;
999 :
END.

{*****}
{constructs 2-way contingency table from 2 window-grid matrices}
{*****}
PROGRAM mat_to_cont(input,output);

LABEL 999;

CONST

    subx_max      = 18; {'integer'}
    suby_max      = 22; {'integer'}
    conx_max      = 2;  {'integer'}
    cony_max      = 2;  {'integer'}

TYPE

    file_name      = varying [80] of char;

VAR

    m1              : array [1..suby_max, 1..subx_max] of integer;
    m2              : array [1..suby_max, 1..subx_max] of integer;
    contingency_table : array [1..cony_max, 1..conx_max] of
integer;
    roota_file      : text;
    rootb_file      : text;
    subx            : integer;
    suby            : integer;
    conx            : integer;
    cony            : integer;

{*****}
{*****}

PROCEDURE do_exit;
begin
    goto 999;
writeln;
end;

{*****}
{*****}
PROCEDURE open_roota_file; {open first read file}

```

```

begin
  open (file_variable := roota_file,      {internal name}
        file_name      := 'mata.dat',      {external name}
        default        := '[c_eve.exptl.intermedata.roots]',
        history        := old,
        error          := continue);

  if status (roota_file) > 0 then
    begin
      writeln ('File A cannot be found ');
      goto 999;
    end;

    reset (roota_file);
    { readln (roota_file); * would get past a header line}
end;
{*****}
PROCEDURE open_rootb_file; {open second read file}
begin
  open (file_variable := rootb_file,
        file_name      := 'matb.dat',
        default        := '[c_eve.exptl.intermedata.roots]',
        history        := old,
        error          := continue);

  if status (rootb_file) > 0 then
    begin
      writeln ('File B cannot be found ');
      goto 999;
    end;

    reset (rootb_file);
    { readln (rootb_file); * would get past a header line}
end;
{*****}
PROCEDURE construct_contingency_table;

begin

contingency_table[1,1] := 0;
contingency_table[1,2] := 0;
contingency_table[2,1] := 0;
contingency_table[2,2] := 0;

suby := 0;
subx := 0;

while suby < suby_max
  do begin
    suby := suby + 1;
    subx := 0;
    while subx < subx_max
      do begin
        subx := subx + 1;
        if m1[suby,subx] = 0
          then conx := 1

```



```

        else
            conx := 2;
        if m2[suby,subx] = 0
            then cony := 1
        else
            cony := 2;

        contingency_table[cony,conx] :=
contingency_table[cony,conx] + 1;

        end;
    end;
end;

{*****}
*****}
PROCEDURE write_file;
begin
    writeln(output, 'CONTINGENCY TABLE');
    writeln (output, '');
    writeln (output, '');
    cony := 1;
    while cony <= cony_max do begin
        conx := 1;
        while conx <= conx_max do begin
            writeln(output, 'species A = ', conx - 1, '; species
B = ',
cony - 1, ': ', contingency_table[cony,conx], 'occurrences');
            conx := conx + 1
        end;
        cony := cony + 1
    end;
end;

{*****}
*****}

{main prog}

begin

open_roota_file; {open first read file}
open_rootb_file; {open second read file}

{write roota_file to array m1}

    for suby := 1 to suby_max do
        begin
            for subx := 1 to subx_max do
                begin
                    read(roota_file, m1[suby,subx]);
{ ***      write(m1[suby,subx]:2);  *** }
                    end;
{ ***      writeln;  *** }
                end;
            end;

{write rootb_file to array m2}

```

```
for suby := 1 to suby_max do
  for subx := 1 to subx_max do
    read(rootb_file, m2[suby, subx]);

{construct the contingency table}
  construct_contingency_table;
  write_file; {write contingency_table to disk}

999 :
end.
```


Part 1 Data

Root observation chamber 1, north window

Treat.	block	window	real-x	real-y	Species
5	1	1	14.5	-7.0	2
5	1	1	14.5	-8.0	2
5	1	1	14.5	-9.0	2
5	1	1	15.0	-5.5	2
5	1	1	15.0	-7.5	2
5	1	1	15.0	-8.5	2
5	1	1	15.0	-11.5	2
5	1	1	15.5	-7.0	2
5	1	1	15.5	-7.0	2
5	1	1	15.5	-8.0	2
5	1	1	15.5	-9.0	2
5	1	1	15.5	-11.0	2
5	1	1	15.5	-12.0	2
5	1	1	16.0	-6.5	2
5	1	1	16.0	-8.5	2
5	1	1	16.5	-7.0	2
5	1	1	16.5	-9.0	2
5	1	1	16.5	-9.0	2
5	1	1	16.5	-10.0	2
5	1	1	16.5	-11.0	2
5	1	1	16.5	-12.0	2
5	1	1	17.0	-7.5	2
5	1	1	17.5	-7.0	2
5	1	1	17.5	-7.0	2
5	1	1	17.5	-7.0	2
5	1	1	17.5	-8.0	2
5	1	1	17.5	-9.0	2
5	1	1	17.5	-10.0	2
5	1	1	17.5	-11.0	2
5	1	1	17.5	-12.0	2
5	1	1	18.0	-5.5	2
5	1	1	18.0	-6.5	2
5	1	1	18.0	-6.5	2
5	1	1	0.0	-0.5	3
5	1	1	0.0	-14.5	3
5	1	1	0.0	-15.5	3
5	1	1	0.0	-16.5	3
5	1	1	0.0	-16.5	3
5	1	1	0.0	-16.5	3
5	1	1	0.0	-17.5	3
5	1	1	0.0	-19.5	3
5	1	1	0.0	-20.5	3
5	1	1	0.0	-21.5	3
5	1	1	0.5	-15.0	3
5	1	1	0.5	-15.0	3
5	1	1	0.5	-16.0	3
5	1	1	0.5	-16.0	3
5	1	1	0.5	-17.0	3
5	1	1	0.5	-17.0	3

5	1	1	0.5	-17.0	3
5	1	1	0.5	-18.0	3
5	1	1	0.5	-19.0	3
5	1	1	0.5	-19.0	3
5	1	1	0.5	-20.0	3
5	1	1	0.5	-21.0	3
5	1	1	1.0	-17.5	3
5	1	1	1.0	-17.5	3
5	1	1	1.0	-18.5	3
5	1	1	1.0	-19.5	3
5	1	1	1.0	-21.5	3
5	1	1	1.5	-22.0	3
5	1	1	1.5	-22.0	3
5	1	1	1.5	-22.0	3
5	1	1	1.5	-22.0	3
5	1	1	2.0	-12.5	3
5	1	1	2.0	-16.5	3
5	1	1	2.0	-16.5	3
5	1	1	2.0	-18.5	3
5	1	1	2.0	-19.5	3
5	1	1	2.0	-20.5	3
5	1	1	3.0	-16.5	3
5	1	1	3.0	-18.5	3
5	1	1	3.0	-18.5	3
5	1	1	3.0	-21.5	3
5	1	1	3.5	-11.0	3
5	1	1	3.5	-12.0	3
5	1	1	3.5	-13.0	3
5	1	1	3.5	-15.0	3
5	1	1	3.5	-16.0	3
5	1	1	3.5	-17.0	3
5	1	1	3.5	-18.0	3
5	1	1	3.5	-19.0	3
5	1	1	4.0	-6.5	3
5	1	1	4.0	-8.5	3
5	1	1	4.0	-15.5	3
5	1	1	4.0	-16.5	3
5	1	1	4.0	-16.5	3
5	1	1	4.0	-16.5	3
5	1	1	4.0	-17.5	3
5	1	1	4.0	-19.5	3
5	1	1	4.0	-21.5	3
5	1	1	4.5	-10.0	3
5	1	1	4.5	-11.0	3
5	1	1	4.5	-17.0	3
5	1	1	4.5	-17.0	3
5	1	1	4.5	-18.0	3
5	1	1	4.5	-22.0	3
5	1	1	5.0	-3.5	3
5	1	1	5.0	-9.5	3
5	1	1	5.0	-16.5	3
5	1	1	5.0	-16.5	3
5	1	1	5.0	-18.5	3
5	1	1	5.5	-9.0	3
5	1	1	5.5	-16.0	3
5	1	1	5.5	-17.0	3

5	1	1	5.5	-17.0	3
5	1	1	5.5	-18.0	3
5	1	1	5.5	-19.0	3
5	1	1	5.5	-20.0	3
5	1	1	5.5	-21.0	3
5	1	1	5.5	-22.0	3
5	1	1	6.0	-16.5	3
5	1	1	6.0	-18.5	3
5	1	1	6.5	-16.0	3
5	1	1	7.0	-16.5	3
5	1	1	7.0	-17.5	3
5	1	1	7.0	-17.5	3
5	1	1	7.0	-18.5	3
5	1	1	7.0	-18.5	3
5	1	1	7.0	-18.5	3
5	1	1	7.0	-19.5	3
5	1	1	7.0	-19.5	3
5	1	1	7.0	-19.5	3
5	1	1	7.0	-21.5	3
5	1	1	7.5	-13.0	3
5	1	1	7.5	-18.0	3
5	1	1	7.5	-18.0	3
5	1	1	7.5	-19.0	3
5	1	1	7.5	-20.0	3
5	1	1	7.5	-21.0	3
5	1	1	8.0	-16.5	3
5	1	1	8.0	-18.5	3
5	1	1	8.0	-19.5	3
5	1	1	8.0	-20.5	3
5	1	1	8.0	-20.5	3
5	1	1	8.0	-21.5	3
5	1	1	8.5	-21.0	3
5	1	1	8.5	-22.0	3
5	1	1	9.0	-19.5	3
5	1	1	9.0	-19.5	3
5	1	1	9.0	-19.5	3
5	1	1	9.0	-21.5	3
5	1	1	9.5	-4.0	3
5	1	1	9.5	-16.0	3
5	1	1	9.5	-18.0	3
5	1	1	9.5	-22.0	3
5	1	1	10.0	-15.5	3
5	1	1	10.0	-16.5	3
5	1	1	10.0	-16.5	3
5	1	1	10.0	-17.5	3
5	1	1	10.0	-18.5	3
5	1	1	10.0	-19.5	3
5	1	1	10.0	-21.5	3
5	1	1	10.5	-6.0	3
5	1	1	10.5	-16.0	3
5	1	1	10.5	-18.0	3
5	1	1	10.5	-22.0	3
5	1	1	11.0	-16.5	3
5	1	1	11.0	-18.5	3
5	1	1	11.0	-19.5	3
5	1	1	11.0	-20.5	3

5	1	1	11.0	-21.5	3
5	1	1	11.0	-21.5	3
5	1	1	11.0	-21.5	3
5	1	1	11.0	-21.5	3
5	1	1	11.5	-19.0	3
5	1	1	11.5	-19.0	3
5	1	1	11.5	-22.0	3
5	1	1	11.5	-22.0	3
5	1	1	12.5	-4.0	3
5	1	1	12.5	-5.0	3
5	1	1	12.5	-6.0	3
5	1	1	12.5	-12.0	3
5	1	1	12.5	-16.0	3
5	1	1	12.5	-20.0	3
5	1	1	12.5	-21.0	3
5	1	1	12.5	-22.0	3
5	1	1	12.5	-22.0	3
5	1	1	12.5	-22.0	3
5	1	1	13.5	-11.0	3
5	1	1	13.5	-13.0	3
5	1	1	13.5	-20.0	3
5	1	1	14.0	-6.5	3
5	1	1	14.0	-13.5	3
5	1	1	14.0	-21.5	3
5	1	1	14.5	-4.0	3
5	1	1	14.5	-14.0	3
5	1	1	15.0	-12.5	3
5	1	1	15.0	-15.5	3
5	1	1	15.0	-20.5	3
5	1	1	15.5	-12.0	3
5	1	1	15.5	-13.0	3
5	1	1	15.5	-15.0	3
5	1	1	15.5	-18.0	3
5	1	1	15.5	-21.0	3
5	1	1	15.5	-22.0	3
5	1	1	16.0	-6.5	3
5	1	1	16.0	-13.5	3
5	1	1	16.0	-15.5	3
5	1	1	16.0	-20.5	3
5	1	1	16.0	-21.5	3
5	1	1	16.5	-18.0	3
5	1	1	16.5	-20.0	3
5	1	1	16.5	-21.0	3
5	1	1	17.0	-18.5	3
5	1	1	17.0	-21.5	3
5	1	1	17.5	-12.0	3
5	1	1	17.5	-22.0	3
5	1	1	18.0	-11.5	3
5	1	1	18.0	-18.5	3
5	1	1	18.0	-18.5	3
5	1	1	18.0	-20.5	3

Root observation chamber 5, north window

Treat.	block	window	real-x	real-y	Species
--------	-------	--------	--------	--------	---------

Treat.	block	window	real-x	real-y	Species
4	1	1	3.5	-14.0	1
4	1	1	5.0	-19.5	1
4	1	1	6.0	-15.5	1
4	1	1	6.0	-16.5	1
4	1	1	7.0	-14.5	1
4	1	1	8.0	-11.5	1
4	1	1	8.0	-14.5	1
4	1	1	8.0	-18.5	1
4	1	1	8.5	-14.0	1
4	1	1	8.5	-14.0	1
4	1	1	8.5	-15.0	1
4	1	1	8.5	-16.0	1
4	1	1	8.5	-16.0	1
4	1	1	8.5	-18.0	1
4	1	1	8.5	-18.0	1
4	1	1	8.5	-19.0	1
4	1	1	8.5	-20.0	1
4	1	1	8.5	-21.0	1
4	1	1	8.5	-22.0	1
4	1	1	9.0	-11.5	1
4	1	1	9.0	-12.5	1
4	1	1	9.0	-12.5	1
4	1	1	9.0	-13.5	1
4	1	1	9.0	-13.5	1
4	1	1	9.0	-15.5	1
4	1	1	9.5	-12.0	1
4	1	1	9.5	-13.0	1
4	1	1	9.5	-15.0	1
4	1	1	10.0	-10.5	1
4	1	1	10.0	-14.5	1
4	1	1	10.5	-10.0	1
4	1	1	10.5	-10.0	1
4	1	1	10.5	-13.0	1
4	1	1	11.0	-9.5	1
4	1	1	11.0	-9.5	1
4	1	1	11.0	-9.5	1
4	1	1	11.0	-11.5	1
4	1	1	11.0	-14.5	1
4	1	1	11.0	-14.5	1
4	1	1	11.5	-9.0	1
4	1	1	11.5	-9.0	1
4	1	1	11.5	-10.0	1
4	1	1	11.5	-14.0	1
4	1	1	12.0	-8.5	1
4	1	1	12.0	-8.5	1
4	1	1	12.5	-2.0	1
4	1	1	12.5	-3.0	1
4	1	1	12.5	-8.0	1
4	1	1	13.0	-7.5	1
4	1	1	13.5	-12.0	1
4	1	1	13.5	-13.0	1
4	1	1	13.5	-13.0	1
4	1	1	13.5	-15.0	1
4	1	1	13.5	-16.0	1
4	1	1	14.0	-9.5	1
4	1	1	14.0	-10.5	1
4	1	1	14.0	-11.5	1

Treat.	block	window	real-x	real-y	Species
4	1	1	14.0	-13.5	1
4	1	1	14.0	-14.5	1
4	1	1	14.5	-10.0	1
4	1	1	14.5	-10.0	1
4	1	1	14.5	-12.0	1
4	1	1	14.5	-13.0	1
4	1	1	16.0	-9.5	1
4	1	1	16.5	-10.0	1
4	1	1	16.5	-10.0	1
4	1	1	16.5	-12.0	1
4	1	1	16.5	-13.0	1
4	1	1	16.5	-14.0	1
4	1	1	16.5	-21.0	1
4	1	1	16.5	-21.0	1
4	1	1	16.5	-21.0	1
4	1	1	16.5	-21.0	1
4	1	1	17.0	-9.5	1
4	1	1	17.0	-9.5	1
4	1	1	17.0	-10.5	1
4	1	1	17.0	-17.5	1
4	1	1	17.0	-18.5	1
4	1	1	17.0	-19.5	1
4	1	1	17.0	-20.5	1
4	1	1	17.0	-20.5	1
4	1	1	17.0	-21.5	1
4	1	1	17.0	-21.5	1
4	1	1	17.0	-21.5	1
4	1	1	17.0	-21.5	1
4	1	1	17.5	-12.0	1
4	1	1	17.5	-13.0	1
4	1	1	17.5	-13.0	1
4	1	1	17.5	-13.0	1
4	1	1	17.5	-13.0	1
4	1	1	17.5	-14.0	1
4	1	1	17.5	-15.0	1
4	1	1	17.5	-16.0	1
4	1	1	17.5	-17.0	1
4	1	1	17.5	-18.0	1
4	1	1	17.5	-19.0	1
4	1	1	17.5	-20.0	1
4	1	1	17.5	-22.0	1
4	1	1	18.0	-12.5	1
4	1	1	18.0	-12.5	1
4	1	1	18.0	-13.5	1
4	1	1	18.0	-17.5	1
4	1	1	18.0	-17.5	1
4	1	1	18.0	-17.5	1
4	1	1	18.0	-18.5	1
4	1	1	18.0	-18.5	1
4	1	1	18.0	-18.5	1
4	1	1	18.0	-18.5	1
4	1	1	18.0	-19.5	1
4	1	1	18.0	-21.5	1
4	1	1	18.0	-21.5	1
4	1	1	18.0	-21.5	1
4	1	1	0.0	-1.5	3
4	1	1	0.0	-1.5	3
4	1	1	0.0	-10.5	3

Treat.	block	window	real-x	real-y	Species
4	1	1	0.0	-11.5	3
4	1	1	0.0	-18.5	3
4	1	1	0.0	-20.5	3
4	1	1	0.5	-2.0	3
4	1	1	0.5	-2.0	3
4	1	1	0.5	-3.0	3
4	1	1	0.5	-4.0	3
4	1	1	0.5	-9.0	3
4	1	1	0.5	-10.0	3
4	1	1	0.5	-10.0	3
4	1	1	0.5	-15.0	3
4	1	1	0.5	-15.0	3
4	1	1	0.5	-17.0	3
4	1	1	0.5	-17.0	3
4	1	1	0.5	-18.0	3
4	1	1	0.5	-18.0	3
4	1	1	0.5	-19.0	3
4	1	1	0.5	-20.0	3
4	1	1	0.5	-21.0	3
4	1	1	0.5	-21.0	3
4	1	1	0.5	-22.0	3
4	1	1	0.5	-22.0	3
4	1	1	1.0	-0.5	3
4	1	1	1.0	-6.5	3
4	1	1	1.0	-14.5	3
4	1	1	1.0	-16.5	3
4	1	1	1.0	-17.5	3
4	1	1	1.0	-17.5	3
4	1	1	1.0	-19.5	3
4	1	1	1.0	-21.5	3
4	1	1	1.5	-7.0	3
4	1	1	1.5	-14.0	3
4	1	1	1.5	-19.0	3
4	1	1	1.5	-20.0	3
4	1	1	2.0	-7.5	3
4	1	1	2.0	-14.5	3
4	1	1	2.0	-14.5	3
4	1	1	2.0	-15.5	3
4	1	1	2.0	-15.5	3
4	1	1	2.0	-15.5	3
4	1	1	2.0	-15.5	3
4	1	1	2.0	-16.5	3
4	1	1	2.0	-16.5	3
4	1	1	2.0	-18.5	3
4	1	1	2.0	-21.5	3
4	1	1	2.0	-21.5	3
4	1	1	2.5	-1.0	3
4	1	1	2.5	-7.0	3
4	1	1	2.5	-12.0	3
4	1	1	2.5	-15.0	3
4	1	1	2.5	-15.0	3
4	1	1	2.5	-15.0	3
4	1	1	2.5	-17.0	3
4	1	1	2.5	-22.0	3
4	1	1	3.0	-14.5	3
4	1	1	3.0	-16.5	3
4	1	1	3.0	-18.5	3

Treat.	block	window	real-x	real-y	Species
4	1	1	3.0	-18.5	3
4	1	1	3.0	-19.5	3
4	1	1	3.5	-6.0	3
4	1	1	3.5	-18.0	3
4	1	1	3.5	-19.0	3
4	1	1	3.5	-20.0	3
4	1	1	3.5	-20.0	3
4	1	1	3.5	-22.0	3
4	1	1	4.0	-18.5	3
4	1	1	4.0	-19.5	3
4	1	1	4.0	-20.5	3
4	1	1	4.0	-20.5	3
4	1	1	4.0	-21.5	3
4	1	1	4.0	-21.5	3
4	1	1	4.5	-10.0	3
4	1	1	4.5	-14.0	3
4	1	1	4.5	-19.0	3
4	1	1	4.5	-20.0	3
4	1	1	4.5	-21.0	3
4	1	1	4.5	-22.0	3
4	1	1	4.5	-22.0	3
4	1	1	5.0	-3.5	3
4	1	1	5.0	-9.5	3
4	1	1	5.0	-12.5	3
4	1	1	5.0	-15.5	3
4	1	1	5.0	-17.5	3
4	1	1	5.0	-20.5	3
4	1	1	5.5	-1.0	3
4	1	1	5.5	-17.0	3
4	1	1	5.5	-17.0	3
4	1	1	5.5	-22.0	3
4	1	1	6.0	-1.5	3
4	1	1	6.0	-18.5	3
4	1	1	6.0	-20.5	3
4	1	1	6.0	-20.5	3
4	1	1	6.0	-21.5	3
4	1	1	6.0	-21.5	3
4	1	1	6.5	-4.0	3
4	1	1	6.5	-12.0	3
4	1	1	6.5	-15.0	3
4	1	1	6.5	-20.0	3
4	1	1	6.5	-20.0	3
4	1	1	6.5	-22.0	3
4	1	1	7.0	-1.5	3
4	1	1	7.0	-4.5	3
4	1	1	7.0	-12.5	3
4	1	1	7.0	-17.5	3
4	1	1	7.0	-18.5	3
4	1	1	7.0	-19.5	3
4	1	1	7.0	-20.5	3
4	1	1	7.5	-1.0	3
4	1	1	7.5	-13.0	3
4	1	1	7.5	-15.0	3
4	1	1	7.5	-17.0	3
4	1	1	7.5	-18.0	3
4	1	1	7.5	-19.0	3
4	1	1	7.5	-21.0	3

Treat.	block	window	real-x	real-y	Species
4	1	1	8.0	-14.5	3
4	1	1	8.0	-15.5	3
4	1	1	8.0	-17.5	3
4	1	1	8.0	-19.5	3
4	1	1	8.5	-15.0	3
4	1	1	8.5	-15.0	3
4	1	1	8.5	-15.0	3
4	1	1	8.5	-16.0	3
4	1	1	8.5	-17.0	3
4	1	1	8.5	-18.0	3
4	1	1	8.5	-18.0	3
4	1	1	8.5	-19.0	3
4	1	1	8.5	-20.0	3
4	1	1	8.5	-21.0	3
4	1	1	8.5	-22.0	3
4	1	1	8.5	-22.0	3
4	1	1	9.0	-14.5	3
4	1	1	9.0	-18.5	3
4	1	1	9.0	-18.5	3
4	1	1	9.0	-20.5	3
4	1	1	9.5	-22.0	3
4	1	1	10.0	-8.5	3
4	1	1	10.0	-9.5	3
4	1	1	10.0	-17.5	3
4	1	1	10.0	-17.5	3
4	1	1	10.0	-21.5	3
4	1	1	10.0	-21.5	3
4	1	1	10.5	-16.0	3
4	1	1	10.5	-17.0	3
4	1	1	10.5	-17.0	3
4	1	1	10.5	-21.0	3
4	1	1	10.5	-22.0	3
4	1	1	10.5	-22.0	3
4	1	1	10.5	-22.0	3
4	1	1	11.0	-3.5	3
4	1	1	11.0	-16.5	3
4	1	1	11.0	-17.5	3
4	1	1	11.0	-18.5	3
4	1	1	11.0	-20.5	3
4	1	1	11.0	-21.5	3
4	1	1	11.0	-21.5	3
4	1	1	11.5	-4.0	3
4	1	1	11.5	-6.0	3
4	1	1	11.5	-10.0	3
4	1	1	11.5	-16.0	3
4	1	1	11.5	-17.0	3
4	1	1	11.5	-17.0	3
4	1	1	11.5	-18.0	3
4	1	1	12.0	-1.5	3
4	1	1	12.0	-2.5	3
4	1	1	12.0	-16.5	3
4	1	1	12.0	-17.5	3
4	1	1	12.0	-18.5	3
4	1	1	12.0	-19.5	3
4	1	1	12.0	-19.5	3
4	1	1	12.0	-20.5	3
4	1	1	12.5	-10.0	3

Treat.	block	window	real-x	real-y	Species
4	1	1	12.5	-12.0	3
4	1	1	12.5	-13.0	3
4	1	1	12.5	-14.0	3
4	1	1	12.5	-15.0	3
4	1	1	12.5	-16.0	3
4	1	1	12.5	-17.0	3
4	1	1	12.5	-18.0	3
4	1	1	12.5	-19.0	3
4	1	1	12.5	-20.0	3
4	1	1	12.5	-21.0	3
4	1	1	12.5	-22.0	3
4	1	1	13.0	-3.5	3
4	1	1	13.0	-8.5	3
4	1	1	13.0	-15.5	3
4	1	1	13.0	-19.5	3
4	1	1	13.5	-2.0	3
4	1	1	13.5	-3.0	3
4	1	1	13.5	-7.0	3
4	1	1	13.5	-9.0	3
4	1	1	13.5	-19.0	3
4	1	1	13.5	-21.0	3
4	1	1	14.0	-1.5	3
4	1	1	14.0	-2.5	3
4	1	1	14.0	-20.5	3
4	1	1	14.0	-21.5	3
4	1	1	14.5	-8.0	3
4	1	1	14.5	-16.0	3
4	1	1	14.5	-16.0	3
4	1	1	14.5	-19.0	3
4	1	1	15.0	-8.5	3
4	1	1	15.0	-13.5	3
4	1	1	15.5	-13.0	3
4	1	1	15.5	-13.0	3
4	1	1	16.0	-17.5	3
4	1	1	16.0	-18.5	3
4	1	1	16.0	-19.5	3
4	1	1	16.5	-22.0	3
4	1	1	17.0	-21.5	3
4	1	1	18.0	-11.5	3
4	1	1	18.0	-14.5	3
4	1	1	18.0	-14.5	3
4	1	1	18.0	-18.5	3
4	1	1	18.0	-20.5	3
4	1	1	18.0	-21.5	3

Root observation chamber 8, north window

Treat.	block	window	real-x	real-y	Species
4	2	1	3.1	-1.0	3
4	2	1	6.4	-1.0	3
4	2	1	8.5	-1.0	3
4	2	1	9.6	-1.0	3
4	2	1	3.5	-2.0	3
4	2	1	4.7	-2.0	3

4	2	1	6.4	-2.0	3
4	2	1	8.9	-2.0	3
4	2	1	3.5	-3.0	3
4	2	1	3.7	-3.0	3
4	2	1	4.4	-3.0	3
4	2	1	6.6	-3.0	3
4	2	1	9.6	-3.0	3
4	2	1	13.3	-3.0	1
4	2	1	0.3	-4.0	3
4	2	1	2.7	-4.0	3
4	2	1	5.7	-4.0	3
4	2	1	6.2	-4.0	3
4	2	1	6.8	-4.0	3
4	2	1	8.4	-4.0	3
4	2	1	9.4	-4.0	3
4	2	1	10.2	-4.0	3
4	2	1	10.7	-4.0	3
4	2	1	12.2	-4.0	3
4	2	1	12.3	-4.0	1
4	2	1	2.1	-5.0	3
4	2	1	2.1	-5.0	3
4	2	1	5.6	-5.0	3
4	2	1	8.3	-5.0	3
4	2	1	9.4	-5.0	3
4	2	1	9.6	-5.0	3
4	2	1	10.8	-5.0	3
4	2	1	11.3	-5.0	1
4	2	1	10.2	-5.0	1
4	2	1	13.8	-5.0	3
4	2	1	1.2	-6.0	3
4	2	1	5.5	-6.0	3
4	2	1	7.4	-6.0	3
4	2	1	10.5	-6.0	3
4	2	1	12.4	-6.0	3
4	2	1	16.3	-6.0	3
4	2	1	16.4	-6.0	3
4	2	1	0.1	-7.0	3
4	2	1	2.6	-7.0	3
4	2	1	8.3	-7.0	3
4	2	1	8.6	-7.0	3
4	2	1	11.8	-7.0	3
4	2	1	12.4	-7.0	3
4	2	1	15.4	-7.0	3
4	2	1	3.2	-8.0	3
4	2	1	6.0	-8.0	3
4	2	1	7.4	-8.0	3
4	2	1	8.3	-8.0	3
4	2	1	13.4	-8.0	3
4	2	1	14.8	-8.0	3
4	2	1	15.1	-8.0	3
4	2	1	18.0	-8.0	3
4	2	1	0.3	-9.0	3
4	2	1	1.4	-9.0	3
4	2	1	4.0	-9.0	3
4	2	1	6.4	-9.0	3
4	2	1	6.8	-9.0	3
4	2	1	7.1	-9.0	3
4	2	1	12.5	-9.0	3

4	2	1	12.7	-9.0	3
4	2	1	14.6	-9.0	1
4	2	1	14.6	-9.0	3
4	2	1	6.7	-10.0	3
4	2	1	7.0	-10.0	3
4	2	1	7.9	-10.0	3
4	2	1	13.8	-10.0	3
4	2	1	13.9	-10.0	1
4	2	1	15.0	-10.0	3
4	2	1	0.4	-11.0	3
4	2	1	5.5	-11.0	3
4	2	1	7.0	-11.0	3
4	2	1	12.1	-11.0	3
4	2	1	13.1	-11.0	3
4	2	1	13.1	-11.0	3
4	2	1	13.2	-11.0	1
4	2	1	13.4	-11.0	1
4	2	1	14.3	-11.0	V
4	2	1	5.9	-12.0	3
4	2	1	7.2	-12.0	3
4	2	1	8.1	-12.0	3
4	2	1	10.0	-12.0	3
4	2	1	12.6	-12.0	1
4	2	1	12.7	-12.0	1
4	2	1	15.4	-12.0	3
4	2	1	15.6	-12.0	3
4	2	1	2.2	-13.0	3
4	2	1	2.3	-13.0	3
4	2	1	3.1	-13.0	3
4	2	1	6.0	-13.0	3
4	2	1	5.9	-13.0	3
4	2	1	7.2	-13.0	3
4	2	1	10.2	-13.0	3
4	2	1	11.8	-13.0	1
4	2	1	12.1	-13.0	1
4	2	1	12.3	-13.0	1
4	2	1	12.5	-13.0	1
4	2	1	4.1	-14.0	1
4	2	1	6.2	-14.0	3
4	2	1	7.2	-14.0	3
4	2	1	9.0	-14.0	3
4	2	1	8.9	-14.0	1
4	2	1	10.4	-14.0	1
4	2	1	11.9	-14.0	1
4	2	1	3.7	-15.0	3
4	2	1	4.8	-15.0	1
4	2	1	4.9	-15.0	3
4	2	1	5.1	-15.0	3
4	2	1	5.1	-15.0	3
4	2	1	10.0	-15.0	1
4	2	1	11.9	-15.0	3
4	2	1	12.2	-15.0	3
4	2	1	1.9	-16.0	3
4	2	1	2.9	-16.0	3
4	2	1	3.6	-16.0	3
4	2	1	4.4	-16.0	3
4	2	1	5.6	-16.0	3
4	2	1	6.4	-16.0	3

4	2	1	8.3	-16.0	1
4	2	1	8.6	-16.0	3
4	2	1	9.6	-16.0	1
4	2	1	9.6	-16.0	3
4	2	1	10.8	-16.0	1
4	2	1	10.8	-16.0	1
4	2	1	11.4	-16.0	3
4	2	1	11.9	-16.0	3
4	2	1	2.0	-17.0	1
4	2	1	2.7	-17.0	1
4	2	1	4.4	-17.0	3
4	2	1	5.0	-17.0	1
4	2	1	5.2	-17.0	1
4	2	1	5.3	-17.0	3
4	2	1	5.9	-17.0	3
4	2	1	6.1	-17.0	3
4	2	1	6.5	-17.0	3
4	2	1	6.5	-17.0	3
4	2	1	9.7	-17.0	1
4	2	1	9.9	-17.0	3
4	2	1	11.3	-17.0	3
4	2	1	11.9	-17.0	3
4	2	1	1.2	-18.0	3
4	2	1	1.4	-18.0	3
4	2	1	2.6	-18.0	3
4	2	1	3.1	-18.0	3
4	2	1	3.5	-18.0	3
4	2	1	4.4	-18.0	3
4	2	1	5.7	-18.0	3
4	2	1	6.2	-18.0	3
4	2	1	6.4	-18.0	3
4	2	1	6.4	-18.0	3
4	2	1	7.4	-18.0	3
4	2	1	9.6	-18.0	1
4	2	1	9.9	-18.0	3
4	2	1	10.8	-18.0	3
4	2	1	11.4	-18.0	3
4	2	1	11.9	-18.0	3
4	2	1	12.2	-18.0	3
4	2	1	16.0	-18.0	3
4	2	1	0.7	-19.0	3
4	2	1	1.0	-19.0	3
4	2	1	2.0	-19.0	3
4	2	1	3.5	-19.0	3
4	2	1	3.9	-19.0	3
4	2	1	4.0	-19.0	3
4	2	1	4.8	-19.0	3
4	2	1	6.5	-19.0	3
4	2	1	7.5	-19.0	3
4	2	1	7.8	-19.0	3
4	2	1	8.1	-19.0	3
4	2	1	9.7	-19.0	1
4	2	1	9.8	-19.0	1
4	2	1	10.0	-19.0	1
4	2	1	10.2	-19.0	1
4	2	1	10.3	-19.0	3
4	2	1	11.1	-19.0	1
4	2	1	11.6	-19.0	3

4	2	1	11.9	-19.0	3
4	2	1	14.7	-19.0	3
4	2	1	15.8	-19.0	1
4	2	1	15.6	-19.0	1
4	2	1	16.5	-19.0	3
4	2	1	17.3	-19.0	3
4	2	1	1.2	-20.0	1
4	2	1	1.5	-20.0	3
4	2	1	2.1	-20.0	3
4	2	1	2.7	-20.0	3
4	2	1	3.3	-20.0	3
4	2	1	6.6	-20.0	3
4	2	1	7.6	-20.0	3
4	2	1	7.8	-20.0	3
4	2	1	8.6	-20.0	1
4	2	1	8.8	-20.0	3
4	2	1	9.5	-20.0	1
4	2	1	9.6	-20.0	1
4	2	1	9.8	-20.0	1
4	2	1	10.1	-20.0	1
4	2	1	10.3	-20.0	3
4	2	1	11.7	-20.0	3
4	2	1	11.9	-20.0	3
4	2	1	15.2	-20.0	3
4	2	1	15.3	-20.0	3
4	2	1	15.4	-20.0	3
4	2	1	15.6	-20.0	1
4	2	1	15.7	-20.0	3
4	2	1	17.2	-20.0	3
4	2	1	17.8	-20.0	3
4	2	1	17.8	-20.0	1
4	2	1	0.9	-21.0	1
4	2	1	1.1	-21.0	3
4	2	1	1.4	-21.0	3
4	2	1	3.8	-21.0	3
4	2	1	6.7	-21.0	3
4	2	1	8.1	-21.0	3
4	2	1	8.3	-21.0	3
4	2	1	8.4	-21.0	3
4	2	1	8.6	-21.0	3
4	2	1	9.4	-21.0	3
4	2	1	9.5	-21.0	1
4	2	1	10.9	-21.0	3
4	2	1	11.4	-21.0	3
4	2	1	11.7	-21.0	3
4	2	1	13.8	-21.0	1
4	2	1	13.9	-21.0	3
4	2	1	14.2	-21.0	1
4	2	1	15.3	-21.0	1
4	2	1	15.5	-21.0	1
4	2	1	16.4	-21.0	3
4	2	1	16.7	-21.0	3
4	2	1	0.4	-22.0	3
4	2	1	0.9	-22.0	3
4	2	1	1.4	-22.0	3
4	2	1	2.5	-22.0	3
4	2	1	4.6	-22.0	3
4	2	1	5.1	-22.0	3

4	2	1	6.9	-22.0	3
4	2	1	8.1	-22.0	1
4	2	1	8.2	-22.0	3
4	2	1	9.4	-22.0	3
4	2	1	9.4	-22.0	1
4	2	1	9.4	-22.0	1
4	2	1	10.3	-22.0	3
4	2	1	11.0	-22.0	3
4	2	1	11.8	-22.0	3
4	2	1	12.4	-22.0	1
4	2	1	13.5	-22.0	3
4	2	1	14.9	-22.0	1
4	2	1	15.0	-22.0	1
4	2	1	15.5	-22.0	3
4	2	1	16.0	-22.0	3
4	2	1	16.2	-22.0	1
4	2	1	17.9	-22.0	3
4	2	1	0.0	-2.5	3
4	2	1	0.0	-7.0	3
4	2	1	0.0	-16.2	3
4	2	1	0.0	-18.5	3
4	2	1	0.0	-18.8	3
4	2	1	0.0	-19.9	3
4	2	1	0.0	-19.9	3
4	2	1	0.0	-21.6	3
4	2	1	1.0	-6.3	3
4	2	1	1.0	-8.8	3
4	2	1	1.0	-11.3	3
4	2	1	1.0	-12.5	3
4	2	1	1.0	-14.1	3
4	2	1	1.0	-19.1	3
4	2	1	1.0	-19.5	1
4	2	1	1.0	-20.4	3
4	2	1	1.0	-20.5	3
4	2	1	1.0	-20.8	1
4	2	1	1.0	-21.1	3
4	2	1	1.0	-21.6	3
4	2	1	1.0	-21.8	3
4	2	1	2.0	-5.0	3
4	2	1	2.0	-5.1	3
4	2	1	2.0	-9.9	3
4	2	1	2.0	-12.8	3
4	2	1	2.0	-12.9	3
4	2	1	2.0	-14.6	3
4	2	1	2.0	-16.0	3
4	2	1	2.0	-17.0	1
4	2	1	2.0	-17.6	3
4	2	1	2.0	-17.6	3
4	2	1	2.0	-19.1	3
4	2	1	2.0	-19.7	3
4	2	1	2.0	-21.3	1
4	2	1	3.0	-1.3	3
4	2	1	3.0	-2.3	3
4	2	1	3.0	-3.6	3
4	2	1	3.0	-7.7	3
4	2	1	3.0	-13.0	3
4	2	1	3.0	-13.2	3
4	2	1	3.0	-16.1	3

4	2	1	3.0	-17.8	3
4	2	1	3.0	-21.6	3
4	2	1	4.0	-2.9	3
4	2	1	4.0	-8.9	3
4	2	1	4.0	-9.7	
4	2	1	4.0	-15.7	3
4	2	1	4.0	-16.7	3
4	2	1	4.0	-18.7	3
4	2	1	4.0	-18.9	3
4	2	1	4.0	-18.9	3
4	2	1	4.0	-19.0	3
4	2	1	4.0	-20.3	3
4	2	1	4.0	-20.5	3
4	2	1	4.0	-21.1	3
4	2	1	4.0	-21.2	3
4	2	1	4.0	-21.5	3
4	2	1	5.0	-1.7	3
4	2	1	5.0	-2.8	3
4	2	1	5.0	-4.1	3
4	2	1	5.0	-9.2	3
4	2	1	5.0	-13.5	3
4	2	1	5.0	-13.6	3
4	2	1	5.0	-14.9	3
4	2	1	5.0	-15.1	3
4	2	1	5.0	-15.2	3
4	2	1	5.0	-15.5	3
4	2	1	5.0	-16.7	3
4	2	1	5.0	-16.9	1
4	2	1	5.0	-17.0	1
4	2	1	5.0	-18.5	3
4	2	1	5.0	-19.1	3
4	2	1	6.0	-1.5	3
4	2	1	6.0	-3.1	3
4	2	1	6.0	-3.9	3
4	2	1	6.0	-5.9	3
4	2	1	6.0	-6.3	3
4	2	1	6.0	-8.0	3
4	2	1	6.0	-10.5	3
4	2	1	6.0	-10.7	3
4	2	1	6.0	-11.8	3
4	2	1	6.0	-12.8	3
4	2	1	6.0	-13.1	3
4	2	1	6.0	-14.9	3
4	2	1	6.0	-16.1	3
4	2	1	6.0	-17.3	3
4	2	1	7.0	-4.5	3
4	2	1	7.0	-4.8	3
4	2	1	7.0	-6.4	3
4	2	1	7.0	-8.7	3
4	2	1	7.0	-9.1	3
4	2	1	7.0	-9.6	3
4	2	1	7.0	-10.0	3
4	2	1	7.0	-10.4	3
4	2	1	7.0	-11.0	3
4	2	1	7.0	-16.4	3
4	2	1	7.0	-19.4	3
4	2	1	7.0	-20.4	3
4	2	1	7.0	-21.4	3

4	2	1	7.0	-21.6	3
4	2	1	7.0	-21.6	3
4	2	1	8.0	-0.4	3
4	2	1	8.0	-3.3	3
4	2	1	8.0	-5.2	3
4	2	1	8.0	-5.7	3
4	2	1	8.0	-7.3	3
4	2	1	8.0	-7.9	3
4	2	1	8.0	-8.3	3
4	2	1	8.0	-10.0	3
4	2	1	8.0	-12.3	3
4	2	1	8.0	-17.4	3
4	2	1	8.0	-19.2	3
4	2	1	8.0	-19.8	3
4	2	1	8.0	-20.9	3
4	2	1	8.0	-21.3	3
4	2	1	8.0	-21.8	3
4	2	1	8.0	-21.9	3
4	2	1	8.0	-21.9	3
4	2	1	9.0	-1.6	3
4	2	1	9.0	-1.6	3
4	2	1	9.0	-4.8	3
4	2	1	9.0	-6.5	3
4	2	1	9.0	-12.3	3
4	2	1	9.0	-12.5	
4	2	1	9.0	-13.5	3
4	2	1	9.0	-14.0	3
4	2	1	9.0	-16.2	1
4	2	1	9.0	-16.1	1
4	2	1	9.0	-19.6	1
4	2	1	9.0	-19.7	1
4	2	1	9.0	-20.9	3
4	2	1	9.0	-21.9	1
4	2	1	10.0	-1.4	3
4	2	1	10.0	-3.4	3
4	2	1	10.0	-3.5	3
4	2	1	10.0	-3.6	3
4	2	1	10.0	-3.8	3
4	2	1	10.0	-4.4	3
4	2	1	10.0	-5.5	3
4	2	1	10.0	-5.6	3
4	2	1	10.0	-5.8	3
4	2	1	10.0	-8.1	3
4	2	1	10.0	-8.3	3
4	2	1	10.0	-10.4	3
4	2	1	10.0	-11.4	3
4	2	1	10.0	-11.9	3
4	2	1	10.0	-12.0	3
4	2	1	10.0	-12.7	
4	2	1	10.0	-15.4	1
4	2	1	10.0	-15.8	1
4	2	1	10.0	-16.6	1
4	2	1	10.0	-17.1	3
4	2	1	10.0	-19.0	1
4	2	1	10.0	-19.0	1
4	2	1	10.0	-19.1	3
4	2	1	10.0	-20.0	1
4	2	1	10.0	-20.4	3

4	2	1	10.0	-20.6	3
4	2	1	11.0	-4.1	3
4	2	1	11.0	-6.5	3
4	2	1	11.0	-6.8	3
4	2	1	11.0	-7.0	3
4	2	1	11.0	-8.6	3
4	2	1	11.0	-13.6	3
4	2	1	11.0	-15.8	3
4	2	1	11.0	-15.9	1
4	2	1	11.0	-19.0	3
4	2	1	11.0	-20.4	1
4	2	1	11.0	-20.5	3
4	2	1	11.0	-20.8	3
4	2	1	12.0	-1.2	3
4	2	1	12.0	-4.4	3
4	2	1	12.0	-4.5	1
4	2	1	12.0	-6.5	3
4	2	1	12.0	-6.6	3
4	2	1	12.0	-7.1	3
4	2	1	12.0	-9.2	3
4	2	1	12.0	-12.6	1
4	2	1	12.0	-14.4	3
4	2	1	12.0	-14.8	3
4	2	1	12.0	-15.5	3
4	2	1	12.0	-17.2	3
4	2	1	12.0	-17.4	3
4	2	1	12.0	-20.8	3
4	2	1	12.0	-20.1	3
4	2	1	13.0	-3.3	1
4	2	1	13.0	-4.7	3
4	2	1	13.0	-5.5	3
4	2	1	13.0	-8.8	3
4	2	1	13.0	-11.1	3
4	2	1	13.0	-11.2	3
4	2	1	13.0	-11.2	1
4	2	1	13.0	-12.2	1
4	2	1	13.0	-21.5	1
4	2	1	14.0	-5.0	3
4	2	1	14.0	-5.5	3
4	2	1	14.0	-9.5	3
4	2	1	14.0	-9.6	3
4	2	1	14.0	-9.6	1
4	2	1	14.0	-15.2	3
4	2	1	14.0	-16.6	3
4	2	1	14.0	-21.1	1
4	2	1	15.0	-6.9	3
4	2	1	15.0	-7.8	3
4	2	1	15.0	-8.1	3
4	2	1	15.0	-8.3	3
4	2	1	15.0	-8.5	3
4	2	1	15.0	-10.0	3
4	2	1	15.0	-20.8	1
4	2	1	15.0	-21.5	1
4	2	1	15.0	-22.0	1
4	2	1	16.0	-6.0	3
4	2	1	16.0	-6.4	3
4	2	1	16.0	-9.1	3
4	2	1	16.0	-10.5	3

4	2	1	16.0	-12.4	3
4	2	1	16.0	-18.0	3
4	2	1	16.0	-18.4	1
4	2	1	16.0	-18.5	1
4	2	1	16.0	-18.5	1
4	2	1	16.0	-18.6	3
4	2	1	16.0	-18.9	3
4	2	1	16.0	-19.8	1
4	2	1	16.0	-20.5	1
4	2	1	16.0	-21.8	3
4	2	1	16.0	-21.9	1
4	2	1	17.0	-7.4	3
4	2	1	17.0	-16.8	3
4	2	1	17.0	-18.5	3
4	2	1	17.0	-19.4	3
4	2	1	17.0	-20.1	3
4	2	1	17.0	-21.1	3
4	2	1	17.0	-21.3	3
4	2	1	18.0	-5.6	3
4	2	1	18.0	-8.1	3
4	2	1	18.0	-13.0	1
4	2	1	18.0	-14.8	1
4	2	1	18.0	-16.1	3
4	2	1	18.0	-18.2	3
4	2	1	18.0	-19.4	3
4	2	1	18.0	-20.0	3
4	2	1	18.0	-20.8	
4	2	1	18.0	-21.6	3

Root observation chamber 9, north window

Treat.	Block	Window	Real-x	Real-y	Species
5	2	1	0.6	-1.0	3
5	2	1	2.7	-1.0	3
5	2	1	5.5	-1.0	3
5	2	1	0.1	-2.0	3
5	2	1	5.2	-3.0	3
5	2	1	5.4	-3.0	3
5	2	1	7.2	-3.0	3
5	2	1	4.3	-4.0	3
5	2	1	6.6	-4.0	3
5	2	1	7.4	-4.0	3
5	2	1	2.2	-5.0	3
5	2	1	5.7	-5.0	3
5	2	1	5.9	-5.0	3
5	2	1	1.9	-6.0	3
5	2	1	7.9	-6.0	3
5	2	1	8.7	-6.0	3
5	2	1	10.6	-6.0	2
5	2	1	14.2	-6.0	2
5	2	1	14.2	-7.0	2
5	2	1	9.1	-8.0	3
5	2	1	14.0	-8.0	2
5	2	1	5.2	-9.0	3
5	2	1	13.8	-9.0	2
5	2	1	16.1	-9.0	2

5	2	1	0.9	-10.0	3
5	2	1	1.1	-10.0	3
5	2	1	4.4	-10.0	3
5	2	1	4.7	-10.0	3
5	2	1	12.8	-10.0	3
5	2	1	15.2	-10.0	3
5	2	1	2.3	-11.0	3
5	2	1	4.0	-11.0	3
5	2	1	6.0	-11.0	3
5	2	1	8.2	-11.0	3
5	2	1	3.2	-12.0	3
5	2	1	8.8	-12.0	3
5	2	1	9.9	-12.0	3
5	2	1	8.8	-12.0	3
5	2	1	0.9	-14.0	3
5	2	1	3.5	-14.0	3
5	2	1	7.7	-14.0	3
5	2	1	7.8	-14.0	3
5	2	1	0.2	-15.0	3
5	2	1	0.4	-15.0	3
5	2	1	0.8	-15.0	3
5	2	1	8.6	-15.0	3
5	2	1	8.5	-15.0	3
5	2	1	2.4	-16.0	3
5	2	1	2.7	-16.0	3
5	2	1	3.0	-16.0	3
5	2	1	3.4	-16.0	3
5	2	1	8.4	-16.0	3
5	2	1	8.6	-16.0	3
5	2	1	9.2	-16.0	3
5	2	1	12.1	-16.0	3
5	2	1	1.1	-17.0	3
5	2	1	3.2	-17.0	3
5	2	1	6.6	-17.0	3
5	2	1	1.0	-18.0	3
5	2	1	2.2	-18.0	3
5	2	1	3.2	-18.0	3
5	2	1	7.3	-18.0	3
5	2	1	0.3	-19.0	3
5	2	1	0.9	-19.0	3
5	2	1	1.5	-19.0	3
5	2	1	3.0	-19.0	3
5	2	1	3.6	-19.0	3
5	2	1	5.2	-19.0	3
5	2	1	5.9	-19.0	3
5	2	1	7.2	-19.0	3
5	2	1	7.3	-19.0	3
5	2	1	7.6	-19.0	3
5	2	1	8.1	-19.0	3
5	2	1	8.8	-19.0	3
5	2	1	11.6	-19.0	3
5	2	1	12.2	-19.0	3
5	2	1	14.4	-19.0	3
5	2	1	15.9	-19.0	3
5	2	1	16.3	-19.0	3
5	2	1	1.4	-20.0	3
5	2	1	1.8	-20.0	3
5	2	1	2.7	-20.0	3

5	2	1	3.6	-20.0	3
5	2	1	5.1	-20.0	3
5	2	1	7.0	-20.0	3
5	2	1	7.4	-20.0	3
5	2	1	7.5	-20.0	3
5	2	1	8.4	-20.0	3
5	2	1	9.7	-20.0	3
5	2	1	12.3	-20.0	3
5	2	1	13.3	-20.0	3
5	2	1	14.9	-20.0	3
5	2	1	17.2	-20.0	3
5	2	1	0.2	-21.0	3
5	2	1	1.1	-21.0	3
5	2	1	3.1	-21.0	3
5	2	1	4.4	-21.0	3
5	2	1	7.1	-21.0	3
5	2	1	7.2	-21.0	3
5	2	1	8.3	-21.0	3
5	2	1	8.5	-21.0	3
5	2	1	8.9	-21.0	3
5	2	1	9.5	-21.0	3
5	2	1	13.5	-21.0	3
5	2	1	14.1	-21.0	3
5	2	1	15.6	-21.0	3
5	2	1	16.3	-21.0	3
5	2	1	16.6	-21.0	3
5	2	1	0.4	-22.0	3
5	2	1	1.1	-22.0	3
5	2	1	2.1	-22.0	3
5	2	1	2.1	-22.0	3
5	2	1	4.9	-22.0	3
5	2	1	5.0	-22.0	3
5	2	1	5.7	-22.0	3
5	2	1	9.1	-22.0	3
5	2	1	9.6	-22.0	3
5	2	1	11.6	-22.0	3
5	2	1	0.0	-1.8	3
5	2	1	0.0	-7.0	3
5	2	1	0.0	-8.7	3
5	2	1	0.0	-13.4	3
5	2	1	0.0	-14.5	3
5	2	1	0.0	-17.9	3
5	2	1	0.0	-18.7	3
5	2	1	0.0	-20.1	3
5	2	1	1.0	-10.0	3
5	2	1	1.0	-10.4	3
5	2	1	1.0	-14.2	3
5	2	1	1.0	-15.2	3
5	2	1	1.0	-17.7	3
5	2	1	1.0	-17.9	3
5	2	1	1.0	-18.5	3
5	2	1	1.0	-18.9	3
5	2	1	1.0	-21.1	3
5	2	1	1.0	-21.9	3
5	2	1	2.0	-5.1	3
5	2	1	2.0	-6.1	3
5	2	1	2.0	-15.1	3
5	2	1	2.0	-17.1	3

5	2	1	2.0	-17.7	3
5	2	1	2.0	-19.6	3
5	2	1	2.0	-21.8	3
5	2	1	3.0	-3.4	3
5	2	1	3.0	-4.8	3
5	2	1	3.0	-16.3	3
5	2	1	3.0	-19.1	3
5	2	1	3.0	-19.5	3
5	2	1	3.0	-21.1	3
5	2	1	4.0	-3.7	3
5	2	1	4.0	-4.4	3
5	2	1	4.0	-6.4	3
5	2	1	4.0	-9.5	3
5	2	1	4.0	-9.6	3
5	2	1	4.0	-11.0	3
5	2	1	4.0	-11.2	3
5	2	1	4.0	-14.8	3
5	2	1	4.0	-16.7	3
5	2	1	4.0	-19.2	3
5	2	1	4.0	-20.8	3
5	2	1	4.0	-21.4	3
5	2	1	5.0	-1.2	3
5	2	1	5.0	-2.6	3
5	2	1	5.0	-3.2	3
5	2	1	5.0	-6.5	3
5	2	1	5.0	-9.5	3
5	2	1	5.0	-8.4	3
5	2	1	5.0	-11.2	3
5	2	1	5.0	-14.4	3
5	2	1	5.0	-18.4	3
5	2	1	5.0	-21.4	3
5	2	1	5.0	-22.0	3
5	2	1	6.0	-1.0	3
5	2	1	6.0	-5.1	3
5	2	1	6.0	-11.0	3
5	2	1	6.0	-12.3	3
5	2	1	6.0	-17.4	3
5	2	1	6.0	-18.4	3
5	2	1	6.0	-19.6	3
5	2	1	7.0	-0.6	3
5	2	1	7.0	-2.5	3
5	2	1	7.0	-3.9	3
5	2	1	7.0	-7.8	3
5	2	1	7.0	-11.1	3
5	2	1	7.0	-12.1	3
5	2	1	7.0	-17.8	3
5	2	1	7.0	-18.2	3
5	2	1	7.0	-19.1	3
5	2	1	7.0	-19.6	3
5	2	1	7.0	-19.9	3
5	2	1	7.0	-20.3	3
5	2	1	7.0	-21.4	3
5	2	1	8.0	-6.0	3
5	2	1	8.0	-10.8	3
5	2	1	8.0	-13.7	3
5	2	1	8.0	-14.5	3
5	2	1	8.0	-15.8	3
5	2	1	8.0	-18.1	3

5	2	1	8.0	-18.9	3
5	2	1	8.0	-19.2	3
5	2	1	8.0	-19.5	3
5	2	1	8.0	-20.9	3
5	2	1	9.0	-1.1	3
5	2	1	9.0	-7.9	3
5	2	1	9.0	-12.8	3
5	2	1	9.0	-15.7	3
5	2	1	9.0	-18.5	3
5	2	1	9.0	-20.7	3
5	2	1	9.0	-21.1	3
5	2	1	9.0	-21.5	3
5	2	1	10.0	-11.3	3
5	2	1	10.0	-11.4	3
5	2	1	10.0	-11.9	3
5	2	1	10.0	-15.2	3
5	2	1	10.0	-21.3	3
5	2	1	11.0	-10.4	3
5	2	1	11.0	-19.2	3
5	2	1	12.0	-15.9	3
5	2	1	12.0	-16.4	3
5	2	1	12.0	-17.4	3
5	2	1	12.0	-18.8	3
5	2	1	12.0	-20.7	3
5	2	1	12.0	-21.5	3
5	2	1	13.0	-10.4	3
5	2	1	13.0	-16.3	3
5	2	1	13.0	-18.9	3
5	2	1	13.0	-20.7	3
5	2	1	13.0	-21.5	3
5	2	1	14.0	-8.0	2
5	2	1	14.0	-18.4	3
5	2	1	14.0	-20.7	3
5	2	1	14.0	-20.9	3
5	2	1	14.0	-21.3	3
5	2	1	14.0	-21.5	3
5	2	1	15.0	-9.9	3
5	2	1	15.0	-16.8	3
5	2	1	15.0	-19.5	3
5	2	1	15.0	-19.3	3
5	2	1	15.0	-20.1	3
5	2	1	15.0	-21.2	3
5	2	1	16.0	-19.0	3
5	2	1	16.0	-19.3	3
5	2	1	16.0	-20.3	3
5	2	1	16.0	-20.8	3
5	2	1	16.0	-21.4	3
5	2	1	17.0	-17.8	3
5	2	1	17.0	-18.5	3
5	2	1	17.0	-19.6	3
5	2	1	17.0	-20.1	3
5	2	1	17.0	-20.5	3
5	2	1	17.0	-20.6	3
5	2	1	17.0	-21.4	3
5	2	1	18.0	-19.2	3
5	2	1	18.0	-20.8	0

Root observation chamber 13, north window

Treat.	Block	Window	Real-x	Real-y	Species
5	3	1	1.8	-3.0	3
5	3	1	6.6	-3.0	3
5	3	1	17.8	-1.0	3
5	3	1	17.8	-2.0	3
5	3	1	6.7	-3.0	3
5	3	1	6.8	-3.0	3
5	3	1	6.1	-5.0	3
5	3	1	6.3	-5.0	3
5	3	1	10.8	-5.0	3
5	3	1	15.6	-5.0	2
5	3	1	17.5	-5.0	2
5	3	1	0.3	-6.0	3
5	3	1	3.4	-6.0	3
5	3	1	13.1	-6.0	2
5	3	1	15.7	-6.0	2
5	3	1	0.0	-7.0	3
5	3	1	1.8	-7.0	3
5	3	1	6.6	-7.0	3
5	3	1	6.8	-7.0	3
5	3	1	7.5	-7.0	3
5	3	1	8.5	-7.0	3
5	3	1	8.6	-7.0	3
5	3	1	12.9	-7.0	2
5	3	1	14.2	-7.0	2
5	3	1	14.3	-7.0	2
5	3	1	4.1	-8.0	3
5	3	1	4.9	-8.0	3
5	3	1	7.3	-8.0	3
5	3	1	7.7	-8.0	3
5	3	1	12.7	-8.0	2
5	3	1	14.1	-8.0	2
5	3	1	14.5	-8.0	2
5	3	1	16.9	-8.0	3
5	3	1	3.7	-9.0	3
5	3	1	4.1	-9.0	3
5	3	1	4.3	-9.0	3
5	3	1	10.9	-9.0	2
5	3	1	12.8	-9.0	2
5	3	1	14.5	-9.0	2
5	3	1	0.7	-10.0	3
5	3	1	2.3	-10.0	3
5	3	1	3.1	-10.0	3
5	3	1	5.3	-10.0	3
5	3	1	9.6	-10.0	3
5	3	1	12.1	-10.0	3
5	3	1	14.6	-10.0	2
5	3	1	15.9	-10.0	3
5	3	1	16.0	-10.0	3
5	3	1	17.8	-10.0	3
5	3	1	0.3	-11.0	3
5	3	1	0.5	-11.0	3
5	3	1	0.9	-11.0	3
5	3	1	3.4	-11.0	3
5	3	1	6.3	-11.0	3

5	3	1	8.4	-11.0	3
5	3	1	11.2	-11.0	3
5	3	1	14.8	-11.0	2
5	3	1	16.4	-11.0	2
5	3	1	2.6	-12.0	3
5	3	1	4.1	-12.0	3
5	3	1	8.0	-12.0	3
5	3	1	8.4	-12.0	3
5	3	1	16.0	-12.0	3
5	3	1	16.0	-12.0	2
5	3	1	17.9	-12.0	3
5	3	1	18.0	-12.0	2
5	3	1	0.5	-13.0	3
5	3	1	1.0	-13.0	3
5	3	1	4.9	-13.0	3
5	3	1	7.7	-13.0	3
5	3	1	8.4	-13.0	3
5	3	1	8.6	-13.0	3
5	3	1	9.2	-13.0	3
5	3	1	9.3	-13.0	3
5	3	1	15.8	-13.0	3
5	3	1	4.3	-14.0	3
5	3	1	4.7	-14.0	3
5	3	1	4.9	-14.0	3
5	3	1	7.4	-14.0	3
5	3	1	7.6	-14.0	3
5	3	1	7.6	-14.0	3
5	3	1	8.4	-14.0	3
5	3	1	10.5	-14.0	2
5	3	1	11.9	-14.0	3
5	3	1	12.2	-14.0	3
5	3	1	12.5	-14.0	3
5	3	1	15.4	-14.0	3
5	3	1	15.6	-14.0	3
5	3	1	17.9	-14.0	2
5	3	1	1.1	-15.0	3
5	3	1	6.9	-15.0	3
5	3	1	7.2	-15.0	3
5	3	1	10.3	-15.0	3
5	3	1	11.7	-15.0	3
5	3	1	16.1	-15.0	3
5	3	1	4.1	-16.0	3
5	3	1	5.5	-16.0	3
5	3	1	7.0	-16.0	3
5	3	1	10.0	-16.0	3
5	3	1	13.5	-16.0	3
5	3	1	14.1	-16.0	3
5	3	1	14.6	-16.0	3
5	3	1	16.0	-16.0	3
5	3	1	16.3	-16.0	3
5	3	1	17.6	-16.0	3
5	3	1	17.6	-16.0	3
5	3	1	0.5	-17.0	3
5	3	1	2.3	-17.0	3
5	3	1	3.8	-17.0	3
5	3	1	4.8	-17.0	3
5	3	1	6.1	-17.0	3
5	3	1	7.4	-17.0	3

5	3	1	9.0	-17.0	3
5	3	1	10.7	-17.0	3
5	3	1	10.7	-17.0	3
5	3	1	11.0	-17.0	3
5	3	1	11.8	-17.0	3
5	3	1	12.1	-17.0	3
5	3	1	13.1	-17.0	3
5	3	1	13.2	-17.0	3
5	3	1	13.8	-17.0	3
5	3	1	14.7	-17.0	3
5	3	1	14.9	-17.0	3
5	3	1	15.3	-17.0	3
5	3	1	15.6	-17.0	3
5	3	1	17.9	-17.0	3
5	3	1	0.9	-18.0	3
5	3	1	2.0	-18.0	3
5	3	1	3.9	-18.0	3
5	3	1	5.0	-18.0	3
5	3	1	5.7	-18.0	3
5	3	1	6.4	-18.0	3
5	3	1	8.2	-18.0	3
5	3	1	9.4	-18.0	3
5	3	1	10.9	-18.0	3
5	3	1	14.4	-18.0	3
5	3	1	15.0	-18.0	3
5	3	1	16.7	-18.0	3
5	3	1	0.3	-19.0	3
5	3	1	0.8	-19.0	3
5	3	1	1.2	-19.0	3
5	3	1	3.4	-19.0	3
5	3	1	4.9	-19.0	3
5	3	1	6.4	-19.0	3
5	3	1	7.9	-19.0	3
5	3	1	8.1	-19.0	3
5	3	1	10.4	-19.0	3
5	3	1	11.2	-19.0	3
5	3	1	11.9	-19.0	3
5	3	1	12.6	-19.0	3
5	3	1	14.8	-19.0	3
5	3	1	15.2	-19.0	3
5	3	1	15.3	-19.0	3
5	3	1	16.4	-19.0	3
5	3	1	17.3	-19.0	3
5	3	1	17.6	-19.0	3
5	3	1	3.3	-20.0	3
5	3	1	6.0	-20.0	3
5	3	1	4.8	-20.0	3
5	3	1	8.5	-20.0	3
5	3	1	12.6	-20.0	3
5	3	1	12.8	-20.0	3
5	3	1	17.2	-20.0	3
5	3	1	1.0	-21.0	3
5	3	1	4.3	-21.0	3
5	3	1	8.3	-21.0	3
5	3	1	9.6	-21.0	3
5	3	1	11.6	-21.0	3
5	3	1	12.6	-21.0	3
5	3	1	13.1	-21.0	3

5	3	1	13.8	-21.0	3
5	3	1	15.0	-21.0	3
5	3	1	16.5	-21.0	3
5	3	1	2.3	-22.0	3
5	3	1	3.6	-22.0	3
5	3	1	4.4	-22.0	3
5	3	1	9.9	-22.0	3
5	3	1	10.2	-22.0	3
5	3	1	12.1	-22.0	3
5	3	1	12.2	-22.0	3
5	3	1	12.5	-22.0	3
5	3	1	14.6	-22.0	3
5	3	1	15.0	-22.0	3
5	3	1	15.1	-22.0	3
5	3	1	17.9	-22.0	3
5	3	1	0.0	-1.2	3
5	3	1	0.0	-6.5	3
5	3	1	0.0	-6.8	3
5	3	1	0.0	-11.5	3
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5	3	1	0.0	-11.9	3
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5	3	1	0.0	-15.5	3
5	3	1	0.0	-15.7	3
5	3	1	0.0	-16.4	3
5	3	1	0.0	-17.6	3
5	3	1	0.0	-19.6	3
5	3	1	0.0	-19.8	3
5	3	1	0.0	-19.9	3
5	3	1	0.0	-20.1	3
5	3	1	0.0	-20.5	3
5	3	1	1.0	-1.7	3
5	3	1	1.0	-5.2	3
5	3	1	1.0	-6.6	3
5	3	1	1.0	-9.2	3
5	3	1	1.0	-10.2	3
5	3	1	1.0	-10.4	3
5	3	1	1.0	-10.6	3
5	3	1	1.0	-12.1	3
5	3	1	1.0	-12.2	3
5	3	1	1.0	-13.0	3
5	3	1	1.0	-13.4	3
5	3	1	1.0	-15.2	3
5	3	1	1.0	-18.2	3
5	3	1	1.0	-18.4	3
5	3	1	1.0	-20.2	3
5	3	1	1.0	-20.9	3
5	3	1	2.0	-1.7	3
5	3	1	2.0	-1.7	3
5	3	1	2.0	-10.3	3
5	3	1	2.0	-11.9	3
5	3	1	2.0	-14.6	3
5	3	1	2.0	-15.9	3
5	3	1	2.0	-16.8	3
5	3	1	2.0	-18.0	3
5	3	1	2.0	-21.4	3
5	3	1	3.0	-9.2	3
5	3	1	3.0	-9.4	3

5	3	1	3.0	-10.1	3
5	3	1	3.0	-11.6	3
5	3	1	3.0	-15.3	3
5	3	1	3.0	-17.3	3
5	3	1	3.0	-17.4	3
5	3	1	3.0	-17.5	3
5	3	1	3.0	-18.4	3
5	3	1	3.0	-19.4	3
5	3	1	4.0	-8.8	3
5	3	1	4.0	-8.9	3
5	3	1	4.0	-11.4	3
5	3	1	4.0	-11.9	3
5	3	1	4.0	-16.8	3
5	3	1	4.0	-17.8	3
5	3	1	4.0	-17.9	3
5	3	1	4.0	-20.0	3
5	3	1	4.0	-21.4	3
5	3	1	4.0	-21.8	3
5	3	1	4.0	-21.8	3
5	3	1	5.0	-7.9	3
5	3	1	5.0	-8.0	3
5	3	1	5.0	-9.6	3
5	3	1	5.0	-12.5	3
5	3	1	5.0	-12.9	3
5	3	1	5.0	-14.1	3
5	3	1	5.0	-14.2	3
5	3	1	5.0	-18.1	3
5	3	1	5.0	-18.2	3
5	3	1	5.0	-19.9	3
5	3	1	6.0	-7.4	3
5	3	1	6.0	-10.6	3
5	3	1	6.0	-13.4	3
5	3	1	6.0	-16.3	3
5	3	1	6.0	-17.1	3
5	3	1	6.0	-18.4	3
5	3	1	6.0	-18.8	3
5	3	1	6.0	-21.4	3
5	3	1	7.0	-1.6	3
5	3	1	7.0	-5.3	3
5	3	1	7.0	-6.5	3
5	3	1	7.0	-6.9	3
5	3	1	7.0	-10.1	3
5	3	1	7.0	-11.4	3
5	3	1	7.0	-12.3	3
5	3	1	7.0	-13.5	3
5	3	1	7.0	-14.3	3
5	3	1	7.0	-15.2	3
5	3	1	7.0	-15.5	3
5	3	1	7.0	-16.0	3
5	3	1	7.0	-16.1	3
5	3	1	8.0	-5.6	3
5	3	1	8.0	-8.2	3
5	3	1	8.0	-11.6	3
5	3	1	8.0	-13.4	3
5	3	1	8.0	-15.4	3
5	3	1	8.0	-18.6	3
5	3	1	9.0	-6.1	3
5	3	1	9.0	-7.1	3

5	3	1	9.0	-7.5	3
5	3	1	9.0	-8.7	3
5	3	1	9.0	-12.3	3
5	3	1	9.0	-12.8	3
5	3	1	9.0	-16.9	3
5	3	1	9.0	-18.6	3
5	3	1	9.0	-20.0	3
5	3	1	9.0	-20.1	3
5	3	1	9.0	-20.5	3
5	3	1	10.0	-7.8	3
5	3	1	10.0	-10.2	3
5	3	1	10.0	-15.9	3
5	3	1	10.0	-16.0	3
5	3	1	10.0	-16.6	3
5	3	1	10.0	-18.7	3
5	3	1	10.0	-19.5	3
5	3	1	10.0	-21.7	3
5	3	1	11.0	-8.8	2
5	3	1	11.0	-11.1	3
5	3	1	11.0	-14.5	3
5	3	1	11.0	-17.0	3
5	3	1	11.0	-18.1	3
5	3	1	11.0	-18.2	3
5	3	1	11.0	-18.4	3
5	3	1	11.0	-19.3	3
5	3	1	11.0	-21.5	3
5	3	1	12.0	-10.2	3
5	3	1	12.0	-12.8	3
5	3	1	12.0	-15.1	3
5	3	1	12.0	-16.9	3
5	3	1	12.0	-17.1	3
5	3	1	12.0	-18.3	3
5	3	1	12.0	-18.8	3
5	3	1	12.0	-18.9	3
5	3	1	12.0	-20.3	3
5	3	1	12.0	-21.9	3
5	3	1	13.0	-6.2	2
5	3	1	13.0	-6.8	2
5	3	1	13.0	-8.1	3
5	3	1	13.0	-8.5	3
5	3	1	13.0	-8.8	3
5	3	1	13.0	-10.8	3
5	3	1	13.0	-15.0	3
5	3	1	13.0	-16.4	3
5	3	1	13.0	-16.9	3
5	3	1	13.0	-16.9	3
5	3	1	13.0	-17.1	3
5	3	1	13.0	-17.4	3
5	3	1	13.0	-17.9	3
5	3	1	13.0	-18.4	3
5	3	1	13.0	-18.6	3
5	3	1	14.0	-6.7	2
5	3	1	14.0	-7.0	2
5	3	1	14.0	-13.6	3
5	3	1	14.0	-13.6	3
5	3	1	14.0	-14.4	3
5	3	1	14.0	-16.4	3
5	3	1	14.0	-17.1	3

5	3	1	14.0	-20.8	3
5	3	1	14.0	-21.2	3
5	3	1	15.0	-13.8	3
5	3	1	15.0	-14.3	3
5	3	1	15.0	-14.8	3
5	3	1	15.0	-15.8	3
5	3	1	15.0	-16.9	3
5	3	1	15.0	-17.1	3
5	3	1	15.0	-17.9	3
5	3	1	15.0	-19.9	3
5	3	1	15.0	-20.7	3
5	3	1	15.0	-21.5	3
5	3	1	15.0	-21.9	3
5	3	1	16.0	-10.3	3
5	3	1	16.0	-12.0	2
5	3	1	16.0	-14.7	3
5	3	1	16.0	-15.2	3
5	3	1	16.0	-15.7	3
5	3	1	16.0	-16.0	3
5	3	1	16.0	-16.1	3
5	3	1	16.0	-16.3	3
5	3	1	16.0	-16.4	3
5	3	1	16.0	-17.4	3
5	3	1	16.0	-20.8	3
5	3	1	16.0	-21.3	3
5	3	1	17.0	-6.2	3
5	3	1	17.0	-7.7	3
5	3	1	17.0	-8.0	3
5	3	1	17.0	-14.9	3
5	3	1	17.0	-15.3	3
5	3	1	17.0	-15.4	3
5	3	1	17.0	-17.5	3
5	3	1	17.0	-18.8	3
5	3	1	17.0	-21.0	3
5	3	1	18.0	-5.8	2
5	3	1	18.0	-9.6	3
5	3	1	18.0	-11.4	2
5	3	1	18.0	-12.4	2
5	3	1	18.0	-12.4	3
5	3	1	18.0	-13.5	2
5	3	1	18.0	-16.6	3
5	3	1	18.0	-16.8	3
5	3	1	18.0	-17.6	3
5	3	1	18.0	-18.5	3
5	3	1	18.0	-18.5	3
5	3	1	18.0	-19.3	3
5	3	1	18.0	-19.9	3
5	3	1	18.0	-20.7	3

Root observation chamber 14, north window

Treat.	Block	Window	Real-x	Real-y	Species
4	3	1	3.1	-1.0	3
4	3	1	4.3	-1.0	3
4	3	1	11.7	-1.0	3
4	3	1	6.4	-2.0	3

4	3	1	8.6	-2.0	3
4	3	1	5.2	-3.0	3
4	3	1	14.7	-3.0	3
4	3	1	5.9	-4.0	3
4	3	1	6.8	-5.0	3
4	3	1	6.9	-5.0	3
4	3	1	11.0	-5.0	3
4	3	1	11.9	-5.0	3
4	3	1	13.0	-5.0	3
4	3	1	0.1	-6.0	3
4	3	1	5.4	-6.0	3
4	3	1	6.4	-6.0	3
4	3	1	8.5	-6.0	3
4	3	1	2.4	-7.0	3
4	3	1	4.2	-7.0	3
4	3	1	5.5	-7.0	3
4	3	1	5.6	-7.0	3
4	3	1	11.0	-7.0	3
4	3	1	12.4	-7.0	3
4	3	1	0.1	-8.0	3
4	3	1	3.4	-8.0	3
4	3	1	3.4	-8.0	3
4	3	1	3.4	-8.0	3
4	3	1	3.9	-8.0	3
4	3	1	4.8	-8.0	3
4	3	1	0.2	-9.0	3
4	3	1	3.6	-9.0	3
4	3	1	4.0	-9.0	3
4	3	1	5.9	-9.0	3
4	3	1	6.9	-9.0	3
4	3	1	12.6	-9.0	3
4	3	1	14.0	-9.0	3
4	3	1	3.6	-10.0	3
4	3	1	6.9	-10.0	3
4	3	1	7.8	-10.0	3
4	3	1	7.9	-10.0	3
4	3	1	2.9	-11.0	3
4	3	1	3.0	-11.0	3
4	3	1	6.0	-11.0	3
4	3	1	6.1	-11.0	1
4	3	1	12.9	-11.0	3
4	3	1	15.6	-11.0	3
4	3	1	16.2	-11.0	3
4	3	1	0.4	-12.0	1
4	3	1	2.1	-12.0	3
4	3	1	2.3	-12.0	3
4	3	1	3.8	-12.0	3
4	3	1	5.5	-12.0	3
4	3	1	6.1	-12.0	3
4	3	1	6.3	-12.0	3
4	3	1	7.4	-12.0	3
4	3	1	13.2	-12.0	3
4	3	1	13.7	-12.0	3
4	3	1	13.9	-12.0	3
4	3	1	15.1	-12.0	3
4	3	1	15.9	-12.0	3
4	3	1	17.5	-12.0	3
4	3	1	1.4	-13.0	3

4	3	1	2.4	-13.0	3
4	3	1	3.4	-13.0	3
4	3	1	3.8	-13.0	3
4	3	1	4.5	-13.0	3
4	3	1	5.5	-13.0	3
4	3	1	6.5	-13.0	3
4	3	1	6.8	-13.0	3
4	3	1	7.2	-13.0	3
4	3	1	7.2	-13.0	3
4	3	1	7.5	-13.0	3
4	3	1	7.7	-13.0	3
4	3	1	7.8	-13.0	3
4	3	1	8.1	-13.0	3
4	3	1	10.8	-13.0	3
4	3	1	13.5	-13.0	3
4	3	1	14.9	-13.0	3
4	3	1	15.8	-13.0	1
4	3	1	17.4	-13.0	3
4	3	1	17.8	-13.0	1
4	3	1	17.9	-13.0	1
4	3	1	0.3	-14.0	3
4	3	1	1.5	-14.0	3
4	3	1	4.2	-14.0	3
4	3	1	4.7	-14.0	3
4	3	1	6.2	-14.0	1
4	3	1	6.2	-14.0	3
4	3	1	6.8	-14.0	3
4	3	1	7.4	-14.0	3
4	3	1	7.3	-14.0	3
4	3	1	10.0	-14.0	3
4	3	1	11.2	-14.0	3
4	3	1	11.4	-14.0	3
4	3	1	13.7	-14.0	3
4	3	1	14.4	-14.0	3
4	3	1	16.4	-14.0	3
4	3	1	17.7	-14.0	1
4	3	1	0.1	-15.0	3
4	3	1	1.5	-15.0	3
4	3	1	3.2	-15.0	3
4	3	1	3.5	-15.0	3
4	3	1	3.7	-15.0	3
4	3	1	5.4	-15.0	3
4	3	1	6.7	-15.0	3
4	3	1	7.3	-15.0	3
4	3	1	8.5	-15.0	3
4	3	1	9.5	-15.0	3
4	3	1	10.8	-15.0	3
4	3	1	15.1	-15.0	3
4	3	1	17.6	-15.0	1
4	3	1	1.3	-16.0	3
4	3	1	1.6	-16.0	3
4	3	1	1.7	-16.0	3
4	3	1	3.0	-16.0	3
4	3	1	6.3	-16.0	3
4	3	1	7.7	-16.0	3
4	3	1	9.2	-16.0	3
4	3	1	9.7	-16.0	3
4	3	1	9.8	-16.0	3

4	3	1	17.4	-16.0	1
4	3	1	17.5	-16.0	1
4	3	1	1.3	-17.0	3
4	3	1	2.3	-17.0	3
4	3	1	3.8	-17.0	3
4	3	1	6.0	-17.0	3
4	3	1	6.2	-17.0	3
4	3	1	6.4	-17.0	3
4	3	1	6.5	-17.0	3
4	3	1	8.6	-17.0	3
4	3	1	13.4	-17.0	3
4	3	1	16.8	-17.0	3
4	3	1	17.4	-17.0	1
4	3	1	0.2	-18.0	3
4	3	1	0.6	-18.0	3
4	3	1	1.3	-18.0	3
4	3	1	4.8	-18.0	3
4	3	1	5.1	-18.0	3
4	3	1	5.1	-18.0	3
4	3	1	5.3	-18.0	3
4	3	1	5.6	-18.0	3
4	3	1	5.9	-18.0	3
4	3	1	7.0	-18.0	3
4	3	1	9.4	-18.0	3
4	3	1	10.7	-18.0	3
4	3	1	17.4	-18.0	1
4	3	1	0.6	-19.0	3
4	3	1	2.4	-19.0	3
4	3	1	6.2	-19.0	3
4	3	1	7.5	-19.0	3
4	3	1	12.5	-19.0	3
4	3	1	13.6	-19.0	3
4	3	1	13.4	-19.0	3
4	3	1	17.0	-19.0	3
4	3	1	17.8	-19.0	3
4	3	1	0.5	-20.0	1
4	3	1	1.3	-20.0	3
4	3	1	2.9	-20.0	3
4	3	1	6.4	-20.0	3
4	3	1	6.7	-20.0	3
4	3	1	7.5	-20.0	3
4	3	1	10.2	-20.0	3
4	3	1	13.7	-20.0	3
4	3	1	16.2	-20.0	3
4	3	1	0.5	-21.0	3
4	3	1	1.0	-21.0	1
4	3	1	2.5	-21.0	3
4	3	1	3.5	-21.0	3
4	3	1	4.6	-21.0	3
4	3	1	8.1	-21.0	3
4	3	1	9.4	-21.0	3
4	3	1	14.7	-21.0	3
4	3	1	15.2	-21.0	3
4	3	1	15.5	-21.0	3
4	3	1	16.2	-21.0	3
4	3	1	17.3	-21.0	1
4	3	1	17.7	-21.0	1
4	3	1	1.6	-22.0	1

4	3	1	4.5	-22.0	3
4	3	1	6.2	-22.0	1
4	3	1	6.3	-22.0	1
4	3	1	6.7	-22.0	3
4	3	1	7.4	-22.0	0
4	3	1	8.8	-22.0	3
4	3	1	10.0	-22.0	3
4	3	1	10.4	-22.0	3
4	3	1	11.9	-22.0	3
4	3	1	15.1	-22.0	3
4	3	1	15.8	-22.0	3
4	3	1	16.1	-22.0	3
4	3	1	17.0	-22.0	1
4	3	1	0.0	-5.8	3
4	3	1	0.0	-6.0	3
4	3	1	0.0	-6.1	3
4	3	1	0.0	-6.2	3
4	3	1	0.0	-7.9	3
4	3	1	0.0	-8.9	3
4	3	1	0.0	-9.6	3
4	3	1	0.0	-17.2	3
4	3	1	0.0	-19.1	1
4	3	1	0.0	-19.2	3
4	3	1	0.0	-19.8	1
4	3	1	1.0	-1.8	3
4	3	1	1.0	-5.2	3
4	3	1	1.0	-5.3	3
4	3	1	1.0	-5.6	3
4	3	1	1.0	-6.0	3
4	3	1	1.0	-6.9	3
4	3	1	1.0	-8.7	3
4	3	1	1.0	-9.8	3
4	3	1	1.0	-14.2	3
4	3	1	1.0	-15.9	3
4	3	1	1.0	-17.4	3
4	3	1	1.0	-19.6	3
4	3	1	1.0	-21.0	1
4	3	1	2.0	-1.4	3
4	3	1	2.0	-1.6	3
4	3	1	2.0	-3.3	3
4	3	1	2.0	-8.5	3
4	3	1	2.0	-8.7	3
4	3	1	2.0	-11.5	3
4	3	1	2.0	-12.7	3
4	3	1	2.0	-13.2	3
4	3	1	2.0	-13.3	3
4	3	1	2.0	-14.2	3
4	3	1	2.0	-14.4	3
4	3	1	2.0	-15.6	3
4	3	1	2.0	-16.1	3
4	3	1	2.0	-19.4	3
4	3	1	3.0	-1.7	3
4	3	1	3.0	-1.9	3
4	3	1	3.0	-6.9	3
4	3	1	3.0	-7.9	3
4	3	1	3.0	-9.1	3
4	3	1	3.0	-10.8	3
4	3	1	3.0	-10.9	3

4	3	1	3.0	-10.9	3
4	3	1	3.0	-11.1	3
4	3	1	3.0	-11.2	3
4	3	1	3.0	-11.6	3
4	3	1	3.0	-13.4	3
4	3	1	3.0	-13.6	3
4	3	1	3.0	-14.9	3
4	3	1	3.0	-15.5	3
4	3	1	3.0	-20.3	3
4	3	1	4.0	-4.0	3
4	3	1	4.0	-4.4	3
4	3	1	4.0	-6.4	3
4	3	1	4.0	-6.9	3
4	3	1	4.0	-8.2	3
4	3	1	4.0	-8.3	3
4	3	1	4.0	-8.4	3
4	3	1	4.0	-8.5	3
4	3	1	4.0	-8.5	3
4	3	1	4.0	-8.9	3
4	3	1	4.0	-9.2	3
4	3	1	4.0	-10.3	3
4	3	1	4.0	-10.3	3
4	3	1	4.0	-10.4	3
4	3	1	4.0	-11.0	3
4	3	1	4.0	-11.1	3
4	3	1	4.0	-11.5	3
4	3	1	4.0	-11.6	3
4	3	1	4.0	-12.2	3
4	3	1	4.0	-13.0	3
4	3	1	4.0	-14.7	3
4	3	1	4.0	-17.3	3
4	3	1	4.0	-17.3	3
4	3	1	4.0	-18.7	3
4	3	1	4.0	-18.8	3
4	3	1	4.0	-19.1	3
4	3	1	4.0	-19.3	3
4	3	1	4.0	-19.4	3
4	3	1	4.0	-20.5	3
4	3	1	4.0	-21.6	3
4	3	1	5.0	-2.4	3
4	3	1	5.0	-2.9	3
4	3	1	5.0	-3.2	3
4	3	1	5.0	-4.7	3
4	3	1	5.0	-8.2	3
4	3	1	5.0	-9.6	3
4	3	1	5.0	-10.7	3
4	3	1	5.0	-10.9	3
4	3	1	5.0	-12.1	1
4	3	1	5.0	-12.9	3
4	3	1	5.0	-14.0	3
4	3	1	5.0	-14.6	3
4	3	1	5.0	-16.2	3
4	3	1	5.0	-17.9	3
4	3	1	6.0	-2.8	3
4	3	1	6.0	-3.4	3
4	3	1	6.0	-3.7	3
4	3	1	6.0	-4.1	3
4	3	1	6.0	-6.0	3

4	3	1	6.0	-6.3	3
4	3	1	6.0	-6.5	3
4	3	1	6.0	-8.4	3
4	3	1	6.0	-8.4	3
4	3	1	6.0	-8.9	3
4	3	1	6.0	-9.4	3
4	3	1	6.0	-10.8	3
4	3	1	6.0	-10.9	3
4	3	1	6.0	-11.0	3
4	3	1	6.0	-11.1	1
4	3	1	6.0	-12.0	3
4	3	1	6.0	-12.1	3
4	3	1	6.0	-13.4	3
4	3	1	6.0	-14.4	3
4	3	1	6.0	-16.2	3
4	3	1	6.0	-17.0	3
4	3	1	6.0	-17.6	3
4	3	1	6.0	-18.8	3
4	3	1	6.0	-19.7	3
4	3	1	7.0	-1.6	3
4	3	1	7.0	-1.6	3
4	3	1	7.0	-4.7	3
4	3	1	7.0	-5.0	3
4	3	1	7.0	-5.2	3
4	3	1	7.0	-5.2	3
4	3	1	7.0	-5.2	3
4	3	1	7.0	-7.5	3
4	3	1	7.0	-8.5	3
4	3	1	7.0	-8.9	3
4	3	1	7.0	-9.3	3
4	3	1	7.0	-9.4	3
4	3	1	7.0	-9.9	3
4	3	1	7.0	-13.0	3
4	3	1	7.0	-13.3	3
4	3	1	7.0	-13.3	3
4	3	1	7.0	-14.1	3
4	3	1	7.0	-14.4	3
4	3	1	7.0	-15.5	3
4	3	1	7.0	-15.7	3
4	3	1	7.0	-18.0	3
4	3	1	7.0	-18.5	3
4	3	1	7.0	-18.7	3
4	3	1	7.0	-21.5	3
4	3	1	7.0	-21.8	3
4	3	1	7.0	-21.9	3
4	3	1	8.0	-4.5	3
4	3	1	8.0	-5.8	3
4	3	1	8.0	-8.4	3
4	3	1	8.0	-8.9	3
4	3	1	8.0	-9.9	3
4	3	1	8.0	-10.8	3
4	3	1	8.0	-12.3	3
4	3	1	8.0	-12.6	3
4	3	1	8.0	-12.9	3
4	3	1	8.0	-13.3	3
4	3	1	8.0	-15.8	3
4	3	1	8.0	-16.7	3
4	3	1	8.0	-18.0	3

4	3	1	8.0	-20.9	3
4	3	1	8.0	-21.1	3
4	3	1	8.0	-21.5	3
4	3	1	9.0	-1.3	3
4	3	1	9.0	-4.3	3
4	3	1	9.0	-5.0	3
4	3	1	9.0	-8.7	3
4	3	1	9.0	-8.8	3
4	3	1	9.0	-10.5	3
4	3	1	9.0	-12.9	3
4	3	1	9.0	-13.4	3
4	3	1	9.0	-13.9	3
4	3	1	9.0	-14.0	3
4	3	1	9.0	-16.3	3
4	3	1	9.0	-16.8	3
4	3	1	9.0	-17.2	3
4	3	1	9.0	-18.0	3
4	3	1	9.0	-18.9	3
4	3	1	9.0	-19.5	3
4	3	1	9.0	-21.5	3
4	3	1	10.0	-0.5	3
4	3	1	10.0	-1.8	3
4	3	1	10.0	-2.8	3
4	3	1	10.0	-3.0	3
4	3	1	10.0	-6.1	3
4	3	1	10.0	-10.5	3
4	3	1	10.0	-11.4	3
4	3	1	10.0	-12.0	3
4	3	1	10.0	-13.5	3
4	3	1	10.0	-14.0	3
4	3	1	10.0	-14.1	3
4	3	1	10.0	-19.4	3
4	3	1	11.0	-2.1	3
4	3	1	11.0	-4.2	3
4	3	1	11.0	-5.0	3
4	3	1	11.0	-5.5	3
4	3	1	11.0	-7.7	3
4	3	1	11.0	-9.7	3
4	3	1	11.0	-10.6	3
4	3	1	11.0	-12.4	3
4	3	1	11.0	-14.5	3
4	3	1	11.0	-16.1	3
4	3	1	11.0	-16.3	3
4	3	1	11.0	-17.5	3
4	3	1	11.0	-19.5	3
4	3	1	11.0	-19.6	3
4	3	1	12.0	-2.6	3
4	3	1	12.0	-4.9	3
4	3	1	12.0	-7.0	3
4	3	1	12.0	-7.1	3
4	3	1	12.0	-9.4	3
4	3	1	12.0	-12.4	3
4	3	1	12.0	-13.6	3
4	3	1	12.0	-16.9	3
4	3	1	12.0	-19.4	3
4	3	1	12.0	-19.7	3
4	3	1	12.0	-21.6	3
4	3	1	12.0	-21.6	3

4	3	1	13.0	-0.4	3
4	3	1	13.0	-5.0	3
4	3	1	13.0	-6.5	3
4	3	1	13.0	-8.2	3
4	3	1	13.0	-10.3	3
4	3	1	13.0	-11.1	3
4	3	1	13.0	-11.3	3
4	3	1	13.0	-11.6	3
4	3	1	13.0	-12.3	3
4	3	1	13.0	-13.4	1
4	3	1	13.0	-14.6	3
4	3	1	13.0	-20.2	3
4	3	1	14.0	-0.9	3
4	3	1	14.0	-1.8	3
4	3	1	14.0	-2.2	3
4	3	1	14.0	-2.9	3
4	3	1	14.0	-3.8	3
4	3	1	14.0	-6.3	3
4	3	1	14.0	-9.0	3
4	3	1	14.0	-9.3	3
4	3	1	14.0	-12.6	3
4	3	1	14.0	-13.8	3
4	3	1	14.0	-18.2	3
4	3	1	14.0	-18.8	1
4	3	1	15.0	-3.1	3
4	3	1	15.0	-12.1	3
4	3	1	15.0	-12.9	3
4	3	1	15.0	-14.9	3
4	3	1	15.0	-15.8	1
4	3	1	15.0	-16.2	3
4	3	1	15.0	-21.1	3
4	3	1	15.0	-21.2	3
4	3	1	16.0	-5.3	3
4	3	1	16.0	-7.4	3
4	3	1	16.0	-8.6	3
4	3	1	16.0	-9.4	3
4	3	1	16.0	-10.3	3
4	3	1	16.0	-11.9	3
4	3	1	16.0	-13.9	3
4	3	1	16.0	-16.5	3
4	3	1	16.0	-19.6	3
4	3	1	16.0	-20.0	3
4	3	1	16.0	-21.9	3
4	3	1	17.0	-4.2	3
4	3	1	17.0	-6.7	3
4	3	1	17.0	-7.3	3
4	3	1	17.0	-13.6	3
4	3	1	17.0	-16.0	1
4	3	1	17.0	-16.3	1
4	3	1	17.0	-18.1	1
4	3	1	17.0	-18.7	3
4	3	1	17.0	-21.9	1
4	3	1	18.0	-3.3	3
4	3	1	18.0	-7.9	3
4	3	1	18.0	-10.3	3
4	3	1	18.0	-11.2	3
4	3	1	18.0	-11.4	3
4	3	1	18.0	-12.0	3

4	3	1	18.0	-16.8	1
4	3	1	18.0	-17.9	1
4	3	1	18.0	-19.5	3

Part 2 Programs

```

PROGRAM INTERFAC (INPUT, OUTPUT);
{   file twin_A structure = BOX X Y SP SIZE GROWTH}
{   note file twin_B is identical}
{   ?? file Special_instructions (inc seed weights, sp shape
factors)}
{   file interface_degrees structure = BOX X Y SP SIZE GROWTH N1
N2 N3 N4 N5 N6}

LABEL 999;

(* CONST *)

TYPE
  common_rec = RECORD
    box      :integer;
    x        :integer;
    y        :integer;
    sp       :integer;
    size     :real;
    growth   :real;
  END;
  output_record = RECORD
    half_rec : common_rec;
    N        : array [1..6] of real;
  END;
  file_name  = varying [80] of char;

VAR
  rec_a, rec_b, in_rec, half_rec      : common_rec;
  twin_a, twin_b                      : text;
{identical files containing 1 size and 1 growth param for each
ind. in a box}
  one_to_one_interface               : real;
  temp_n                             : array [1..6] of real;
  (* interface degree between 1 individual and 6 species*)
  out_rec                            : output_record;
  out_file                           : text;
  rec_valid                          : boolean;
{*****}
{***** PROCEDURES *****}
{*****}
PROCEDURE do_exit;
BEGIN
  goto 999;
  writeln;
END;
{*****}
PROCEDURE open_twin_a;
BEGIN
  open (file_variable := twin_a, {internal name}
        file_name     := 'twin_a.dat', {external name}

```

```

        default      := '[c_eve.expt1.raw_data.expt3a]',
        history      := old,
        error        := continue);

if status (twin_a) > 0 then
begin
    writeln (output, 'File twin_a cannot be found ');
    goto 999;
end;

RESET (twin_a);
readln(twin_a); {to get past the header line}
END;
{*****}
PROCEDURE open_twin_b;
BEGIN
    open (file_variable := twin_b,      {internal name}
          file_name     := 'twin_b.dat', {external name}
          default        := '[c_eve.expt1.raw_data.expt3a]',
          history        := old,
          error          := continue);

    if status (twin_b) > 0 then
    begin
        writeln (output, 'File twin_b cannot be found ');
        goto 999;
    end;

    reset (twin_b);
    READLN(twin_b); {to get past the header line}
END;
{*****}
PROCEDURE open_out_file;
BEGIN
    open (file_variable := out_file,      {internal name}
          file_name     := 'interface_degrees.dat', {external
name}
          default        := '[c_eve.expt1.intermedata.int3]',
          history        := new,
          error          := continue);

    IF STATUS (out_file) > 0 THEN BEGIN
        writeln ('File interface_degrees.dat error status: ',
status (out_file));
        goto 999;
    END;

    REWRITE (out_file);
END;
{*****}

PROCEDURE zeroize_temp_N_array;
var i : integer;
BEGIN
    for i:= 1 to 6 do
        temp_n[i] := 0;
    END;

```



```

{*****}
PROCEDURE chk_rec;
(*make sure this version corresponds to calculate_interface
version *)
BEGIN
    rec_valid := true;
    IF
        ((rec_b.x = rec_a.x) and (rec_b.y = rec_a.y))
        OR (rec_b.sp < 1) OR (rec_b.sp > 6)
        OR (rec_b.size < 0)
        OR (rec_b.growth < 0)
    THEN
        rec_valid := false;
    END;
{*****}

PROCEDURE calculate_interface;
(* uses (size * size / distance squared) *)
(*BEGIN
    one_to_one_interface := (rec_a.size*rec_b.size) /
        ((rec_a.x-rec_b.x)**2+(rec_a.y-rec_b.y)**2);
    END;
*)

(* uses (1 / distance squared) *)
BEGIN
    one_to_one_interface :=
        1 / ((rec_a.x-rec_b.x)**2+(rec_a.y-rec_b.y)**2);
END;
{*****}
PROCEDURE write_temp_N_array; {to output file}
VAR
    i:integer;
BEGIN
    half_rec := rec_a;
    FOR i := 1 TO 6 DO BEGIN
        out_rec.n[i] := temp_n[i];
    END;
    WITH rec_a DO
        WRITE (out_file, box, x, y, sp, size, growth);
    FOR i := 1 TO 6 DO BEGIN
        WRITE (out_file, out_rec.n[i]);
    END;
    WRITELN (out_file);
    (* ??? *)
    END;
{*****}

BEGIN {MAIN PROG}

    open_twin_a;
    open_twin_b;
    {??** OPEN input file Special_instructions}
    open_out_file;
    REPEAT

        RESET (twin_b);
        READLN(twin_b); {to get past the header line}

        zeroize_temp_N_array;

```

```

    WITH rec_a DO {saves needing "rec_a.box etc. in readln st.}
      READLN(twin_a, box, x, y, sp, size, growth);
    REPEAT
      WITH rec_b DO
        READLN(twin_b, box, x, y, sp, size, growth);
        chk_rec; (* check record is valid for
calculate_interface*)
        one_to_one_interface := 0;
        IF rec_valid THEN BEGIN
          calculate_interface;
        END;
        temp_n[rec_b.sp] := temp_n[rec_b.sp] +
one_to_one_interface;
      UNTIL EOF(twin_b);
      write_temp_N_array;
    UNTIL(EOF(twin_a));
999:
END.

* compute absolute height growth rates.
COMPUTE ahgr2 = (th2 - th1) / 7.
COMPUTE ahgr3 = (th3 - th2) / 7.
COMPUTE ahgr4 = (th4 - th3) / 7.
COMPUTE ahgr5 = (th5 - th4) / 7.
COMPUTE ahgr6 = (th6 - th5) / 8.
COMPUTE ahgr7 = (th7 - th6) / 7.
COMPUTE ahgr8 = (th8 - th7) / 7.

PROCESS IF (box=1).
COMPUTE ahgr9 = (th9 - th8) / 16.

PROCESS IF (box=2).
COMPUTE ahgr9 = (th9 - th8) / 17.

PROCESS IF (box=3).
COMPUTE ahgr9 = (th9 - th8) / 19.

* compute relative height growth rates.
COMPUTE rhgr2 = ahgr2 / th1.
COMPUTE rhgr3 = ahgr3 / th2.
COMPUTE rhgr4 = ahgr4 / th3.
COMPUTE rhgr5 = ahgr5 / th4.
COMPUTE rhgr6 = ahgr6 / th5.
COMPUTE rhgr7 = ahgr7 / th6.
COMPUTE rhgr8 = ahgr8 / th7.
COMPUTE rhgr9 = ahgr9 / th8.

```

```

*** ZIC.INC: Compute Z-scores for the interface coefficients
***.
*** n1 TO n6 on the basis of pooled distribution of all six
***.
*** interface coefficients.
***.
TITLE 'Compute Z-scores for the interface coefficients'.
GET FILE = '3a_d01.sys'
/DROP = dat_ht TO th8 ahgr2 TO rhgr9.
MISSING VALUES n1 TO n6 (0).
COMPUTE i_Sp = 0.
COMPUTE i_c = 0.
SAVE OUTFILE = '3a_d01.tmp'
/COMPRESSED.
COMPUTE i_Sp = 1.
COMPUTE i_c = n1.
SAVE OUTFILE = 'n1.tmp'.
GET FILE = '3a_d01.tmp'.
COMPUTE i_Sp = 2.
COMPUTE i_c = n2.
SAVE OUTFILE = 'n2.tmp'.
GET FILE = '3a_d01.tmp'.
COMPUTE i_Sp = 3.
COMPUTE i_c = n3.
SAVE OUTFILE = 'n3.tmp'.
GET FILE = '3a_d01.tmp'.
COMPUTE i_Sp = 4.
COMPUTE i_c = n4.
SAVE OUTFILE = 'n4.tmp'.
GET FILE = '3a_d01.tmp'.
COMPUTE i_Sp = 5.
COMPUTE i_c = n5.
SAVE OUTFILE = 'n5.tmp'.
GET FILE = '3a_d01.tmp'.
COMPUTE i_Sp = 6.
COMPUTE i_c = n6.
SAVE OUTFILE = 'n6.tmp'.
GET FILE = 'n5.tmp'.
JOIN ADD
/FILE = 'n1.tmp'
/FILE = 'n2.tmp'
/FILE = 'n3.tmp'
/FILE = 'n4.tmp'
/FILE = *.
JOIN ADD
/FILE = *
/FILE = 'n6.tmp'.
DESCRIPTIVES i_c
/OPTIONS = 3.
COMPUTE zn1 = 0.
COMPUTE zn2 = 0.
COMPUTE zn3 = 0.
COMPUTE zn4 = 0.
COMPUTE zn5 = 0.
COMPUTE zn6 = 0.
IF (i_Sp = 1) zn1 = zi_c.
IF (i_Sp = 2) zn2 = zi_c.
IF (i_Sp = 3) zn3 = zi_c.
IF (i_Sp = 4) zn4 = zi_c.
IF (i_Sp = 5) zn5 = zi_c.

```

```

IF (i_Sp = 6) zn6 = zi_c.
PROCESS IF (i_Sp = 1).
SAVE OUTFILE = 'zn1.tmp'
/DROP = n1 TO n6.
PROCESS IF (i_Sp = 2).
SAVE OUTFILE = 'zn2.tmp'
/DROP = n1 TO n6.
PROCESS IF (i_Sp = 3).
SAVE OUTFILE = 'zn3.tmp'
/DROP = n1 TO n6.
PROCESS IF (i_Sp = 4).
SAVE OUTFILE = 'zn4.tmp'
/DROP = n1 TO n6.
PROCESS IF (i_Sp = 5).
SAVE OUTFILE = 'zn5.tmp'
/DROP = n1 TO n6.
PROCESS IF (i_Sp = 6).
SAVE OUTFILE = 'zn6.tmp'
/DROP = n1 TO n6.
JOIN ADD FILE = 'zn1.tmp'
/FILE = 'zn2.tmp'
/FILE = 'zn3.tmp'
/FILE = 'zn4.tmp'
/FILE = 'zn5.tmp'.
JOIN ADD FILE = *
/FILE = 'zn6.tmp'.
SORT CASES BY sp box x y.
IF (MISSING(zn1)) zn1 = 0.
IF (MISSING(zn2)) zn2 = 0.
IF (MISSING(zn3)) zn3 = 0.
IF (MISSING(zn4)) zn4 = 0.
IF (MISSING(zn5)) zn5 = 0.
IF (MISSING(zn6)) zn6 = 0.
AGGREGATE OUTFILE = *
/BREAK = sp box x y
/zn1 'N1 Zscore (pooled)' = SUM(zn1)
/zn2 'N2 Zscore (pooled)' = SUM(zn2)
/zn3 'N3 Zscore (pooled)' = SUM(zn3)
/zn4 'N4 Zscore (pooled)' = SUM(zn4)
/zn5 'N5 Zscore (pooled)' = SUM(zn5)
/zn6 'N6 Zscore (pooled)' = SUM(zn6).
MISSING VALUE zn1 TO zn6 (0).
SAVE OUTFILE = 'zic.sys'
/COMPRESSED.

```

```

SET ECHO ON /MORE OFF.
SET LISTING = 'regr113.lis'.
*** REGR113.INC: USE ZSCORES TO ENABLE SIMULTANEOUS
***.
*** TREATMENT OF DIFFERENT SPECIES AND DIFFERENT TIMES.
***.
*** Outliers (any interface coefficient GE 0.1) excluded.
***.
*** Interface coefficient values of zero defined missing.
***.
*** Species represented by dummy vars: baseline = beetroot.
***.
*** Use one box or all three with dummy vars for box.
***.
*** This procedure differs from regr12 only in using
***.
*** Z-scores of interface coefficients (from zic.inc)
***.
TITLE "ZSCORE REGRESSIONS of ZTH on ZN1 TO ZN6: ALL BOXES".
GET FILE = '3a_d01.sys'
/DROP = dat_ht TO h5 h6 TO w9 rw9 rhgr2 TO rhgr9.
SORT CASES BY sp box x y.
JOIN MATCH
/TABLE = 'zic.sys'
/FILE = *
/BY sp box x y.

*** calculate Z-scores: ***.
DESCRIPTIVES th2 th3 th4 th5 th6 th7 th8 th9
              t5 t9
              ahgr2 ahgr3 ahgr4 ahgr5 ahgr6 ahgr7 ahgr8 ahgr9
/OPTION = 3.
*** NOTE: baseline is Beetroot (since n greatest). ***.
COMPUTE d_sp1 = 0.
COMPUTE d_sp3 = 0.
COMPUTE d_sp4 = 0.
COMPUTE d_sp5 = 0.
COMPUTE d_sp6 = 0.
IF (sp = 1) d_sp1 = 1.
IF (sp = 3) d_sp3 = 1.
IF (sp = 4) d_sp4 = 1.
IF (sp = 5) d_sp5 = 1.
IF (sp = 6) d_sp6 = 1.
*** NOTE: baseline is box 3. ***.
COMPUTE d_box1 = 0.
COMPUTE d_box2 = 0.
IF (box = 1) d_box1 = 1.
IF (box = 2) d_box2 = 1.
*** remove interface coefficient outliers ***.
COMPUTE max_n = n1.
IF (n2 GT max_n) max_n = n2.
IF (n3 GT max_n) max_n = n3.
IF (n4 GT max_n) max_n = n4.
IF (n5 GT max_n) max_n = n5.
IF (n6 GT max_n) max_n = n6.
SELECT IF (max_n LT 0.1).
MISSING VALUE n1 TO n6 zn1 TO zn6 (0).
SAVE OUTFILE = '3a_d01.tmp'.

```

```

*****

```

```

** .
*****
** .
*****
** .

SUBTITLE "Week 2 Height Zscore: all species".
REGRESSION VARIABLES = d_sp1 TO d_sp6
                     d_box1 d_box2
                     zn1 TO zn6 zth2

/STATISTICS = LINE
/DEPENDENT = zth2
/METHOD = BACKWARDS
/STATISTICS = R
/DEPENDENT = zth2
/METHOD = TEST = (zn5).
*** mark.
*****
** .
SUBTITLE "Week 3 Height Zscore: all species".
REGRESSION VARIABLES = d_sp1 TO d_sp6
                     d_box1 d_box2
                     zn1 TO zn6 zth3

/STATISTICS = LINE
/DEPENDENT = zth3
/METHOD = BACKWARDS
/STATISTICS = R
/DEPENDENT = zth3
/METHOD = TEST = (zn1 zn4 zn5).
*****
** .
SUBTITLE "Week 4 Height Zscore: all species".
REGRESSION VARIABLES = d_sp1 TO d_sp6
                     d_box1 d_box2
                     zn1 TO zn6 zth4

/STATISTICS = LINE
/DEPENDENT = zth4
/METHOD = BACKWARDS
/STATISTICS = R
/DEPENDENT = zth4
/METHOD = TEST = (zn1 zn4 zn5).
*****
** .
SUBTITLE "Week 5 Height Zscore: all species".
REGRESSION VARIABLES = d_sp1 TO d_sp6
                     d_box1 d_box2
                     zn1 TO zn6 zth5

/STATISTICS = LINE
/DEPENDENT = zth5
/METHOD = BACKWARDS
/STATISTICS = R
/DEPENDENT = zth5
/METHOD = TEST = (zn4 zn5).

*****
** .
SELECT IF (sp NE 5).
*****
** .
SUBTITLE "Week 6 Height Zscore: all species except 5".

```

```

REGRESSION VARIABLES = d_sp1 TO d_sp4 d_sp6
                      d_box1 d_box2
                      zn1 TO zn6 zth6

/STATISTICS = LINE
/DEPENDENT = zth6
/METHOD = BACKWARDS
/STATISTICS = R
/DEPENDENT = zth6
/METHOD = TEST = (zn4).
*****
**.
SUBTITLE "Week 7 Height Zscore: all species except 5".
REGRESSION VARIABLES = d_sp1 TO d_sp4 d_sp6
                      d_box1 d_box2
                      zn1 TO zn6 zth7

/STATISTICS = LINE
/DEPENDENT = zth7
/METHOD = BACKWARDS
/STATISTICS = R
/DEPENDENT = zth7
/METHOD = TEST = (zn4).
*****
**.
SUBTITLE "Week 8 Height Zscore: all species except 5".
REGRESSION VARIABLES = d_sp1 TO d_sp4 d_sp6
                      d_box1 d_box2
                      zn1 TO zn6 zth8

/STATISTICS = LINE
/DEPENDENT = zth8
/METHOD = BACKWARDS
/STATISTICS = R
/DEPENDENT = zth8
/METHOD = TEST = (zn3 zn4).
*****
**.
SUBTITLE "Week 9 Height Zscore: all species except 5".
REGRESSION VARIABLES = d_sp1 TO d_sp4 d_sp6
                      d_box1 d_box2
                      zn1 TO zn6 zth9

/STATISTICS = LINE
/DEPENDENT = zth9
/METHOD = BACKWARDS
/STATISTICS = R
/DEPENDENT = zth9
/METHOD = TEST = (zn3 zn4).
*****
**.
*****
**.
*****
**.
TITLE "ZSCORE REGRESSIONS of ZAHGR on ZN1 TO ZN6: ALL BOXES".
GET FILE = '3a_d01.tmp'.

SUBTITLE "Week 2 Height Growth Rate Zscore: all species".
REGRESSION VARIABLES = d_sp1 TO d_sp6
                      d_box1 d_box2
                      zn1 TO zn6 zahgr2

/STATISTICS = LINE
/DEPENDENT = zahgr2

```

```

/METHOD = BACKWARDS
/STATISTICS = R
/DEPENDENT = zahgr2
/METHOD = TEST = (zn5 zn6).
*****
**.
SUBTITLE "Week 3 Height Growth Rate Zscore: all species".
REGRESSION VARIABLES = d_sp1 TO d_sp6
                      d_box1 d_box2
                      zn1 TO zn6 zahgr3

/STATISTICS = LINE
/DEPENDENT = zahgr3
/METHOD = BACKWARDS
/STATISTICS = R
/DEPENDENT = zahgr3
/METHOD = TEST = (zn1 zn4 zn5).
*****
**.
SUBTITLE "Week 4 Height Growth Rate Zscore: all species".
REGRESSION VARIABLES = d_sp1 TO d_sp6
                      d_box1 d_box2
                      zn1 TO zn6 zahgr4

/STATISTICS = LINE
/DEPENDENT = zahgr4
/METHOD = BACKWARDS
/STATISTICS = R
/DEPENDENT = zahgr4
/METHOD = TEST = (zn4).
*****
**.
SUBTITLE "Week 5 Height Growth Rate Zscore: all species".
REGRESSION VARIABLES = d_sp1 TO d_sp6
                      d_box1 d_box2
                      zn1 TO zn6 zahgr5

/STATISTICS = LINE
/DEPENDENT = zahgr5
/METHOD = BACKWARDS.
* /STATISTICS = R
* /DEPENDENT = zahgr5
* /METHOD = TEST = (). ***No ICs left in eqn to test.

*****
**.
SELECT IF (sp NE 5).
*****
**.
SUBTITLE "Week 6 Height Growth Rate Zscore: all species except
5".
REGRESSION VARIABLES = d_sp1 TO d_sp4 d_sp6
                      d_box1 d_box2
                      zn1 TO zn6 zahgr6

/STATISTICS = LINE
/DEPENDENT = zahgr6
/METHOD = BACKWARDS
/STATISTICS = R
/DEPENDENT = zahgr6
/METHOD = TEST = (zn4 zn5).
*****
**.
SUBTITLE "Week 7 Height Growth Rate Zscore: all species except

```



```

5".
REGRESSION VARIABLES = d_sp1 TO d_sp4 d_sp6
                      d_box1 d_box2
                      zn1 TO zn6 zahgr7

/STATISTICS = LINE
/DEPENDENT = zahgr7
/METHOD = BACKWARDS
/STATISTICS = R
/DEPENDENT = zahgr7
/METHOD = TEST = (zn5).
*****
**
SUBTITLE "Week 8 Height Growth Rate Zscore: all species except
5".
REGRESSION VARIABLES = d_sp1 TO d_sp4 d_sp6
                      d_box1 d_box2
                      zn1 TO zn6 zahgr8

/STATISTICS = LINE
/DEPENDENT = zahgr8
/METHOD = BACKWARDS.
* /STATISTICS = R
* /DEPENDENT = zahgr8
* /METHOD = TEST = (). *** no ICs left to test.
*****
**
SUBTITLE "Week 9 Height Growth Rate Zscore: all species except
5".
REGRESSION VARIABLES = d_sp1 TO d_sp4 d_sp6
                      d_box1 d_box2
                      zn1 TO zn6 zahgr9

/STATISTICS = LINE
/DEPENDENT = zahgr9
/METHOD = BACKWARDS
/STATISTICS = R
/DEPENDENT = zahgr9
/METHOD = TEST = (zn3).

```

Part 2 Data

BOX	X	Y
SP	DAT_HT	H1
H2	H3	H4
H5	T5	H6
H7	H7_LLL	H8
H9	R9	C9
W9	T9	RW9
TH1	TH2	TH3
TH4	TH5	TH6
TH7	TH9	TH8
N1	N2	N3
N4	N5	N6

Variable: BOX
No value labels
Missing: * None *

Label: * No label *
Type: Number Width: 8 Dec: 2

Variable: X
No value labels
Missing: * None *

Label: * No label *
Type: Number Width: 8 Dec: 2

Variable: Y
No value labels
Missing: * None *

Label: * No label *
Type: Number Width: 8 Dec: 2

Variable: SP
Value labels follow
Missing: * None *

Label: * No label *
Type: Number Width: 8 Dec: 2

1.00	Leek
3.00	Buttercup
5.00	Broad Bean

2.00	Beetroot
4.00	Marigold
6.00	Endive

Variable: DAT_HT
No value labels
Missing: * None *

Label: * No label *
Type: Number Width: 8 Dec: 2

Variable: H2
No value labels
Missing: -9.00

Label: Ht/cm above datum at n wks
Type: Number Width: 8 Dec: 2

Variable: H3
No value labels
Missing: -9.00

Label: Ht/cm above datum at n wks
Type: Number Width: 8 Dec: 2

Variable: H4
No value labels
Missing: -9.00

Label: Ht/cm above datum at n wks
Type: Number Width: 8 Dec: 2

Variable: H5
No value labels
Missing: -9.00

Label: Ht/cm above datum at n wks
Type: Number Width: 8 Dec: 2

Variable: H6
No value labels
Missing: -9.00

Label: Ht/cm above datum at n wks
Type: Number Width: 8 Dec: 2

Variable: H7
No value labels

Label: Ht/cm above datum at n wks
Type: Number Width: 8 Dec: 2

Missing: -9.00

Variable: H8
No value labels
Missing: -9.00

Label: Ht/cm above datum at n wks
Type: Number Width: 8 Dec: 2

Variable: H9
cutting
No value labels
Missing: -9.00

Label: Ht/cm above sl - msrd after
Type: Number Width: 8 Dec: 2

Variable: R9
No value labels
Missing: * None *

Label: Len/cm of thickest rt
Type: Number Width: 8 Dec: 2

Variable: C9
No value labels
Missing: * None *

Label: Girth/cm of beetroot
Type: Number Width: 8 Dec: 2

Variable: W9
No value labels
Missing: * None *

Label: F. Wt/g whole plant
Type: Number Width: 8 Dec: 2

Variable: T9
No value labels
Missing: * None *

Label: F. Wt/g of shoots
Type: Number Width: 8 Dec: 2

Variable: RW9
No value labels
Missing: * None *

Label: F. Wt/g of roots
Type: Number Width: 8 Dec: 2

Variable: N1
No value labels
Missing: * None *

Label: interference coeff. w/ sp. 1
Type: Number Width: 8 Dec: 2

Variable: N2
No value labels
Missing: * None *

Label: interference coeff. w/ sp. 2
Type: Number Width: 8 Dec: 2

Variable: N3
No value labels
Missing: * None *

Label: interference coeff. w/ sp. 3
Type: Number Width: 8 Dec: 2

Variable: N4
No value labels
Missing: * None *

Label: interference coeff. w/ sp. 4
Type: Number Width: 8 Dec: 2

Variable: N5
No value labels
Missing: * None *

Label: interference coeff. w/ sp. 5
Type: Number Width: 8 Dec: 2

Variable: N6
No value labels
Missing: * None *

Label: interference coeff. w/ sp. 6
Type: Number Width: 8 Dec: 2

Variable: AHGR2
No value labels
Missing: * None *

Label: height growth rate # 2
Type: Number Width: 8 Dec: 2

Variable: AHGR3

Label: height growth rate # 3

No value labels Type: Number Width: 8 Dec: 2
Missing: * None *

Variable: AHGR4 Label: height growth rate # 4
No value labels Type: Number Width: 8 Dec: 2
Missing: * None *

Variable: AHGR5 Label: height growth rate # 5
No value labels Type: Number Width: 8 Dec: 2
Missing: * None *

Variable: AHGR6 Label: height growth rate # 6
No value labels Type: Number Width: 8 Dec: 2
Missing: * None *

Variable: AHGR7 Label: height growth rate # 7
No value labels Type: Number Width: 8 Dec: 2
Missing: * None *

Variable: AHGR8 Label: height growth rate # 8
No value labels Type: Number Width: 8 Dec: 2
Missing: * None *

Variable: AHGR9 Label: height growth rate # 9
No value labels Type: Number Width: 8 Dec: 2
Missing: * None *

Columns 1 to 7

CASE_ NO	BOX	X	Y	SP	DAT_H T	H2
1	1.00	28.00	.00	4.00	3.80	-9.00
2	1.00	31.00	1.00	2.00	3.90	1.60
3	1.00	29.00	4.00	4.00	3.90	.70
4	1.00	37.00	4.00	1.00	3.90	1.00
5	1.00	13.00	6.00	2.00	4.00	.60
6	1.00	22.00	6.00	5.00	4.00	18.50
7	1.00	26.00	6.00	1.00	4.00	.10
8	1.00	3.00	8.00	2.00	3.80	.70
9	1.00	29.00	11.00	6.00	3.90	.70
10	1.00	13.00	12.00	3.00	3.90	-.50
11	1.00	8.00	13.00	6.00	3.90	2.30
12	1.00	15.00	14.00	5.00	3.90	18.80
13	1.00	9.00	15.00	4.00	3.90	.50
14	1.00	51.00	20.00	3.00	3.90	-9.00
15	1.00	21.00	21.00	5.00	3.90	14.60
16	1.00	43.00	21.00	2.00	3.90	.80
17	1.00	36.00	22.00	4.00	3.90	.50
18	1.00	4.00	23.00	3.00	3.90	-1.60
19	1.00	23.00	27.00	3.00	3.90	6.80
20	1.00	30.00	29.00	5.00	3.90	13.70
21	1.00	34.00	33.00	6.00	3.90	1.00
22	1.00	33.00	35.00	1.00	3.90	2.80
23	1.00	46.00	36.00	3.00	3.90	-1.50
24	1.00	27.00	39.00	1.00	3.90	-9.00
25	1.00	46.00	39.00	6.00	4.00	-9.00

26	1.00	47.00	39.00	2.00	4.00	1.10
27	1.00	1.00	41.00	4.00	3.8	-9.00
28	1.00	5.00	43.00	3.00	3.80	3.90
29	1.00	24.00	43.00	1.00	3.90	-9.00
30	1.00	16.00	44.00	2.00	3.80	-9.00
31	1.00	30.00	44.00	5.00	3.90	18.80
32	1.00	44.00	45.00	5.00	4.00	13.70
33	1.00	3.00	46.00	3.00	3.70	3.40
34	1.00	45.00	47.00	2.00	4.00	2.30
35	1.00	1.00	48.00	2.00	3.70	1.80
36	1.00	33.00	48.00	1.00	4.00	1.10
37	1.00	25.00	49.00	4.00	3.90	-1.80
38	1.00	44.00	51.00	6.00	4.00	-9.00
39	1.00	3.00	52.00	4.00	3.70	1.60
40	1.00	11.00	55.00	3.00	3.80	-.90
41	1.00	14.00	55.00	6.00	3.90	-9.00
42	1.00	37.00	56.00	2.00	4.00	3.00
43	1.00	7.00	59.00	6.00	3.90	1.30
44	1.00	14.00	59.00	5.00	3.90	16.40
45	1.00	51.00	59.00	5.00	4.10	16.70
46	1.00	13.00	70.00	4.00	4.00	-9.00
47	1.00	44.00	70.00	3.00	4.20	2.30
48	1.00	10.00	72.00	4.00	4.00	.50
49	1.00	10.00	74.00	6.00	4.00	-9.00
50	1.00	21.00	75.00	3.00	4.10	-2.00
51	1.00	26.00	78.00	1.00	4.20	1.80
52	1.00	6.00	80.00	1.00	4.00	1.30
53	1.00	18.00	80.00	6.00	4.10	-9.00
54	1.00	40.00	80.00	6.00	4.30	2.30
55	1.00	50.00	80.00	1.00	4.30	.20
56	1.00	1.00	82.00	2.00	4.00	-9.00
57	1.00	37.00	84.00	4.00	4.30	-.30
58	1.00	10.00	85.00	2.00	4.00	-.20
59	1.00	30.00	86.00	5.00	4.20	18.00
60	1.00	38.00	86.00	1.00	4.30	2.80
61	1.00	10.00	87.00	6.00	4.00	1.00
62	1.00	15.00	87.00	1.00	4.10	-9.00
63	1.00	17.00	87.00	4.00	4.10	.30
64	1.00	43.00	87.00	3.00	4.30	3.70
65	1.00	28.00	88.00	3.00	4.20	4.30
66	1.00	34.00	91.00	5.00	4.30	17.50
67	1.00	47.00	92.00	5.00	4.40	18.60
68	1.00	48.00	93.00	2.00	4.50	2.60
69	1.00	23.00	94.00	1.00	4.20	-9.00
70	1.00	22.00	97.00	4.00	4.20	1.60
71	1.00	5.00	98.00	6.00	4.10	.00
72	1.00	50.00	106.00	5.00	4.80	7.00
73	2.00	50.00	2.00	5.00	3.90	14.20
74	2.00	8.00	3.00	6.00	4.00	-1.60
75	2.00	44.00	3.00	4.00	3.90	-9.00
76	2.00	29.00	5.00	1.00	3.90	1.40
77	2.00	17.00	6.00	1.00	3.90	3.50
78	2.00	31.00	7.00	4.00	3.90	-9.00
79	2.00	34.00	7.00	5.00	3.90	19.60
80	2.00	10.00	10.00	3.00	4.00	.10
81	2.00	32.00	10.00	5.00	3.90	21.80
82	2.00	8.00	11.00	3.00	4.00	-.50
83	2.00	45.00	11.00	4.00	4.00	2.40

84	2.00	1.00	14.00	1.00	4.00	4.00
85	2.00	19.00	16.00	4.00	4.00	-9.00
86	2.00	4.00	17.00	1.00	4.00	1.00
87	2.00	25.00	19.00	6.00	4.00	.80
88	2.00	12.00	21.00	5.00	4.00	15.10
89	2.00	2.00	23.00	4.00	4.00	2.40
90	2.00	50.00	24.00	3.00	3.80	4.60
91	2.00	42.00	25.00	5.00	3.90	16.00
92	2.00	34.00	27.00	2.00	3.90	1.90
93	2.00	15.00	28.00	6.00	4.00	-9.00
94	2.00	10.00	29.00	6.00	4.00	1.10
95	2.00	13.00	31.00	1.00	4.00	.20
96	2.00	7.00	33.00	4.00	4.00	-9.00
97	2.00	13.00	34.00	4.00	4.00	-9.00
98	2.00	39.00	35.00	5.00	3.90	20.00
99	2.00	23.00	40.00	6.00	4.00	-9.00
100	2.00	28.00	40.00	5.00	4.00	18.50
101	2.00	21.00	42.00	6.00	4.00	-.20
102	2.00	12.00	43.00	5.00	4.00	12.50
103	2.00	27.00	44.00	4.00	4.00	-3.30
104	2.00	4.00	48.00	1.00	3.90	-1.00
105	2.00	31.00	49.00	4.00	4.00	2.60
106	2.00	43.00	51.00	3.00	4.00	1.90
107	2.00	31.00	53.00	3.00	4.00	-1.40
108	2.00	30.00	54.00	2.00	4.00	-.30
109	2.00	20.00	55.00	1.00	4.00	2.40
110	2.00	45.00	56.00	2.00	3.90	1.70
111	2.00	40.00	60.00	2.00	4.00	1.20
112	2.00	16.00	61.00	5.00	3.90	19.00
113	2.00	34.00	62.00	6.00	4.10	1.40
114	2.00	37.00	67.00	6.00	4.10	2.40
115	2.00	5.00	68.00	2.00	3.90	-9.00
116	2.00	13.00	69.00	5.00	3.90	21.70
117	2.00	6.00	71.00	1.00	3.90	4.70
118	2.00	51.00	72.00	1.00	4.00	2.50
119	2.00	33.00	73.00	1.00	4.10	-9.00
120	2.00	18.00	75.00	2.00	4.00	1.80
121	2.00	4.00	76.00	6.00	4.00	2.10
122	2.00	29.00	77.00	3.00	4.10	2.70
123	2.00	32.00	78.00	3.00	4.10	-1.50
124	2.00	10.00	83.00	3.00	4.10	4.30
125	2.00	40.00	83.00	4.00	4.00	-9.00
126	2.00	31.00	84.00	6.00	4.00	1.90
127	2.00	9.00	85.00	6.00	4.10	-1.10
128	2.00	50.00	85.00	1.00	4.00	5.00
129	2.00	25.00	86.00	2.00	4.10	-2.00
130	2.00	4.00	87.00	3.00	4.20	-2.90
131	2.00	9.00	89.00	3.00	4.20	-1.30
132	2.00	18.00	92.00	3.00	4.10	2.60
133	2.00	22.00	92.00	6.00	4.10	-9.00
134	2.00	1.00	93.00	4.00	4.30	-9.00
135	2.00	50.00	93.00	2.00	3.90	-9.00
136	2.00	1.00	94.00	3.00	4.30	-1.80
137	2.00	38.00	95.00	4.00	3.90	1.10
138	2.00	14.00	98.00	5.00	4.20	12.40
139	2.00	6.00	101.00	2.00	4.30	4.20
140	2.00	31.00	103.00	2.00	4.00	.40
141	2.00	11.00	105.00	1.00	4.20	.40

142	2.00	18.00	105.00	2.00	4.10	-2.60
143	2.00	45.00	105.00	2.00	3.80	2.30
144	2.00	52.00	106.00	5.00	3.80	13.90
145	3.00	7.00	.00	4.00	4.40	-9.00
146	3.00	36.00	3.00	1.00	4.30	.90
147	3.00	24.00	5.00	5.00	4.40	14.00
148	3.00	11.00	7.00	2.00	4.40	.10
149	3.00	12.00	7.00	2.00	4.40	2.00
150	3.00	19.00	7.00	5.00	4.40	14.00
151	3.00	35.00	8.00	1.00	4.30	1.80
152	3.00	5.00	10.00	3.00	4.40	-.70
153	3.00	27.00	10.00	3.00	4.30	-1.40
154	3.00	36.00	17.00	6.00	4.30	-9.00
155	3.00	44.00	18.00	5.00	4.30	17.30
156	3.00	49.00	19.00	4.00	4.20	2.60
157	3.00	25.00	22.00	1.00	4.30	.40
158	3.00	46.00	22.00	6.00	4.20	.20
159	3.00	5.00	24.00	2.00	4.40	-.60
160	3.00	29.00	24.00	1.00	4.30	1.30
161	3.00	31.00	24.00	2.00	4.30	2.20
162	3.00	49.00	25.00	6.00	4.20	.60
163	3.00	4.00	26.00	1.00	4.40	-9.00
164	3.00	11.00	29.00	3.00	4.40	-1.90
165	3.00	28.00	29.00	5.00	4.30	18.30
166	3.00	15.00	30.00	4.00	4.40	.00
167	3.00	11.00	32.00	4.00	4.40	.80
168	3.00	9.00	33.00	2.00	4.40	1.30
169	3.00	27.00	34.00	5.00	4.30	18.10
170	3.00	22.00	35.00	6.00	4.30	2.70
171	3.00	29.00	36.00	6.00	4.30	1.70
172	3.00	39.00	37.00	6.00	4.20	2.00
173	3.00	34.00	38.00	4.00	4.20	2.50
174	3.00	12.00	39.00	2.00	4.40	-9.00
175	3.00	23.00	39.00	3.00	4.30	.60
176	3.00	20.00	40.00	5.00	4.30	17.30
177	3.00	33.00	43.00	4.00	4.20	1.90
178	3.00	43.00	44.00	4.00	4.20	1.40
179	3.00	45.00	45.00	3.00	4.20	3.80
180	3.00	35.00	47.00	4.00	4.20	1.80
181	3.00	6.00	48.00	1.00	4.30	-.50
182	3.00	8.00	48.00	4.00	4.30	-9.00
183	3.00	35.00	52.00	6.00	4.20	.60
184	3.00	39.00	54.00	3.00	4.20	2.40
185	3.00	35.00	55.00	3.00	4.20	-3.00
186	3.00	31.00	58.00	2.00	4.20	.50
187	3.00	52.00	58.00	6.00	4.20	2.60
188	3.00	7.00	63.00	3.00	4.20	.10
189	3.00	24.00	63.00	2.00	4.20	.60
190	3.00	45.00	64.00	5.00	4.20	15.90
191	3.00	49.00	64.00	1.00	4.20	-9.00
192	3.00	14.00	66.00	6.00	4.20	-9.00
193	3.00	23.00	66.00	1.00	4.20	4.00
194	3.00	25.00	67.00	5.00	4.20	17.50
195	3.00	13.00	69.00	1.00	4.20	.50
196	3.00	33.00	71.00	1.00	4.20	-1.10
197	3.00	42.00	73.00	6.00	4.20	2.70
198	3.00	35.00	77.00	6.00	4.20	1.00
199	3.00	40.00	77.00	5.00	4.20	24.30

200	3.00	.00	80.00	4.00	4.20	-9.00
201	3.00	3.00	80.00	1.00	4.20	-9.00
202	3.00	2.00	86.00	6.00	4.10	-9.00
203	3.00	20.00	88.00	3.00	4.20	-1.00
204	3.00	35.00	89.00	2.00	4.20	-2.40
205	3.00	44.00	89.00	2.00	4.20	.00
206	3.00	42.00	91.00	5.00	4.20	15.90
207	3.00	10.00	96.00	2.00	4.10	-9.00
208	3.00	28.00	96.00	4.00	4.30	2.60
209	3.00	17.00	97.00	2.00	4.20	1.50
210	3.00	35.00	97.00	3.00	4.30	-.80
211	3.00	46.00	98.00	3.00	4.20	3.70
212	3.00	26.00	100.00	4.00	4.30	-.20
213	3.00	11.00	101.00	5.00	4.10	13.60
214	3.00	46.00	101.00	1.00	4.20	-3.00
215	3.00	2.00	105.00	3.00	4.00	.00
216	3.00	51.00	105.00	5.00	4.20	11.00

Columns 8 to 13

CASE_ NO	H3	H4	H5	H6	H7	H8
1	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
2	6.50	14.20	19.20	21.00	24.40	24.60
3	4.10	9.10	11.80	13.60	15.30	15.70
4	4.40	7.50	8.60	13.90	22.10	22.10
5	5.20	12.00	15.80	18.40	22.40	22.20
6	34.00	46.40	59.90	.	.	.
7	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
8	5.70	11.20	15.30	16.60	21.50	21.50
9	5.30	11.10	13.60	15.10	16.40	21.30
10	1.10	3.60	6.30	9.20	11.60	11.80
11	5.40	9.90	13.80	16.50	19.80	24.50
12	28.10	41.10	51.90	.	.	.
13	2.90	7.30	10.50	13.50	14.50	14.30
14	-3.90	-2.40	-1.80	.30	1.00	1.60
15	29.50	42.80	56.70	.	.	.
16	7.00	14.30	19.90	22.00	45.30	25.90
17	4.20	9.60	12.50	14.10	16.10	15.50
18	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
19	8.20	12.20	12.40	14.60	15.50	15.70
20	26.60	43.40	53.80	.	.	.
21	4.90	8.30	14.80	15.10	13.70	19.50
22	8.40	9.10	10.10	9.70	11.50	10.60
23	-1.00	.50	2.20	3.20	6.60	7.90
24	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
25	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
26	6.10	12.70	17.10	18.20	22.00	22.10
27	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
28	6.50	10.20	12.10	12.80	14.60	14.80
29	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
30	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
31	32.80	44.10	53.90	.	.	.
32	23.70	39.00	49.40	.	.	.
33	5.30	10.50	10.40	13.20	12.80	13.50
34	6.10	14.80	18.60	19.90	21.30	21.70

35	5.40	11.10	16.40	20.00	23.30	22.10
36	8.90	12.50	14.10	14.50	14.90	17.20
37	.00	2.40	5.80	6.50	9.60	10.60
38	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
39	5.20	8.90	13.30	15.30	17.50	16.20
40	1.50	3.90	8.20	10.80	12.90	13.00
41	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
42	10.00	17.90	21.20	22.20	22.20	23.30
43	5.10	8.80	15.60	17.80	17.90	24.90
44	31.00	44.60	55.40	.	.	.
45	26.80	40.90	49.60	.	.	.
46	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
47	4.00	7.00	12.00	13.10	15.40	14.70
48	3.50	7.20	12.80	14.10	16.70	16.10
49	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
50	.30	3.50	6.20	8.50	12.80	12.10
51	10.20	13.10	13.80	18.90	21.50	22.20
52	9.50	14.10	14.80	19.40	24.70	24.80
53	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
54	7.10	13.00	17.40	18.40	18.10	26.10
55	6.90	9.20	9.30	12.20	18.20	18.50
56	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
57	1.80	8.50	11.50	12.60	12.00	13.30
58	3.40	8.40	13.40	17.20	21.40	21.20
59	33.00	48.80	60.40	.	.	.
60	10.00	11.90	13.00	16.00	16.70	16.80
61	5.30	10.50	13.50	16.00	17.60	23.00
62	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
63	4.60	8.00	13.80	14.90	19.50	19.60
64	8.60	15.40	15.40	18.30	18.10	18.00
65	6.30	11.50	15.40	16.50	19.30	19.40
66	29.40	39.80	50.40	.	.	.
67	33.30	46.60	58.60	.	.	.
68	7.60	16.10	19.50	18.10	20.70	21.20
69	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
70	4.60	8.80	12.20	14.10	16.50	15.30
71	3.80	7.50	11.90	13.80	16.50	21.80
72	15.00	24.90	36.10	.	.	.
73	25.20	38.60	47.40	.	.	.
74	1.40	5.00	7.50	9.70	11.00	15.50
75	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
76	8.50	10.30	10.80	11.20	13.80	15.70
77	10.30	12.80	18.30	19.00	20.20	21.60
78	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
79	38.60	51.40	58.60	.	.	.
80	1.50	4.80	6.30	6.60	12.40	12.80
81	35.90	48.90	61.10	.	.	.
82	2.10	4.20	7.00	7.40	12.60	12.50
83	5.80	9.80	11.90	13.40	13.50	13.20
84	13.10	14.20	14.10	18.60	20.00	21.00
85	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
86	6.60	7.30	9.90	12.90	15.80	15.70
87	5.10	9.90	13.10	13.70	13.60	19.90
88	28.10	41.00	54.70	.	.	.
89	6.10	9.20	12.40	14.40	14.30	13.80
90	7.00	9.90	11.00	-9.00	15.10	15.50
91	34.20	48.80	58.30	.	.	.
92	8.30	13.80	19.50	20.60	21.90	22.10

93	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
94	5.80	9.80	14.70	15.00	15.80	21.00
95	3.50	7.00	8.40	8.40	11.30	13.50
96	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
97	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
98	37.00	50.70	63.50	.	.	.
99	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
100	33.90	50.40	64.50	.	.	.
101	3.50	7.90	11.70	12.30	13.00	17.30
102	35.60	50.50	63.90	.	.	.
103	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
104	.90	3.30	6.60	7.60	10.60	13.20
105	5.60	11.20	14.40	15.10	15.60	16.30
106	4.60	10.80	13.50	16.00	17.20	16.20
107	1.30	3.30	5.70	8.30	10.70	14.40
108	4.40	9.20	13.50	15.70	19.00	20.40
109	8.50	7.50	10.70	12.30	13.00	15.70
110	8.10	17.70	21.50	23.30	27.40	27.40
111	7.50	14.20	20.50	22.20	24.20	24.50
112	37.80	53.50	70.30	.	.	.
113	6.00	10.10	16.20	17.00	17.80	22.00
114	6.10	11.70	16.00	16.80	18.10	23.70
115	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
116	37.00	50.90	65.80	.	.	.
117	11.40	12.50	18.50	20.30	22.40	22.70
118	9.40	10.30	16.20	18.70	19.00	19.20
119	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
120	7.80	13.90	19.00	19.70	22.80	23.60
121	5.90	9.90	14.30	15.00	17.60	21.80
122	3.10	5.20	11.50	13.80	15.80	16.50
123	2.10	4.60	6.80	11.70	14.20	15.10
124	7.80	14.00	15.50	15.90	22.50	17.50
125	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
126	5.60	11.00	14.30	16.50	17.80	24.50
127	1.30	6.00	10.30	13.20	15.30	19.70
128	12.00	13.30	17.50	20.90	23.60	25.30
129	.10	4.90	8.00	8.70	11.70	11.60
130	-.50	3.00	5.40	6.50	10.10	10.30
131	-.70	.00	2.30	4.00	7.70	7.40
132	5.90	9.50	12.80	14.00	13.60	13.60
133	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
134	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
135	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
136	.60	3.00	5.50	6.70	8.20	8.20
137	4.00	8.80	13.10	15.10	16.50	16.50
138	21.90	33.70	47.20	.	.	.
139	11.50	17.80	23.00	22.70	23.70	23.40
140	5.10	9.00	17.20	20.00	20.60	20.30
141	5.10	7.80	8.70	10.50	14.10	14.30
142	-1.50	17.70	4.70	5.30	5.50	5.20
143	7.60	11.80	17.60	18.60	22.20	22.00
144	23.50	34.10	46.30	.	.	.
145	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
146	7.30	12.50	12.90	14.40	18.30	24.00
147	31.70	40.00	51.40	.	.	.
148	3.00	7.10	12.60	15.70	19.30	19.70
149	8.50	12.00	21.00	23.50	24.80	24.60
150	26.90	35.50	43.70	.	.	.

151	10.20	11.60	17.70	19.70	21.60	24.60
152	-.30	1.60	4.50	5.40	6.70	7.00
153	-1.50	-1.60	.30	.90	1.50	2.40
154	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
155	31.60	41.10	50.10	.	.	.
156	-.90	1.40	3.40	4.20	8.60	9.90
157	7.00	9.10	9.80	10.90	14.90	17.90
158	5.40	11.60	13.80	14.90	16.30	21.30
159	2.10	6.80	12.70	15.40	20.50	21.50
160	8.60	11.40	11.30	15.00	15.00	15.40
161	10.80	13.50	18.50	21.00	23.80	25.00
162	4.40	9.60	13.40	15.00	15.80	21.60
163	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
164	-2.00	.30	2.30	4.50	8.10	9.20
165	33.60	47.50	62.20	.	.	.
166	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
167	4.10	8.20	11.90	14.70	18.00	18.40
168	8.00	12.00	19.90	21.10	26.20	27.40
169	34.90	52.10	69.90	.	.	.
170	6.70	12.60	17.20	17.30	19.20	24.00
171	4.30	9.70	10.70	12.10	13.60	16.10
172	6.80	13.30	15.50	17.60	19.70	24.90
173	6.40	11.60	16.30	18.00	18.50	18.50
174	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
175	4.10	5.80	5.90	6.00	4.60	7.40
176	33.40	48.00	61.90	.	.	.
177	5.60	11.20	16.50	17.40	17.50	17.40
178	4.90	9.70	14.00	15.20	18.20	17.10
179	8.00	13.00	18.60	20.10	20.20	22.40
180	6.50	10.50	15.10	16.40	16.90	16.20
181	1.30	3.60	4.10	7.10	10.70	12.20
182	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
183	4.90	11.10	14.70	15.70	18.60	24.00
184	3.90	5.60	8.50	10.60	13.50	13.50
185	-2.00	-1.50	1.00	1.70	6.70	8.10
186	4.90	12.30	16.70	17.00	21.60	22.00
187	.40	4.60	6.00	8.10	11.80	16.00
188	2.10	4.50	8.00	9.00	10.90	12.00
189	7.40	11.90	18.00	18.20	21.50	23.00
190	28.60	44.80	57.40	.	.	.
191	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
192	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
193	13.60	14.40	17.10	21.00	22.90	31.20
194	34.90	48.00	61.60	.	.	.
195	6.40	8.30	8.60	10.60	14.00	19.70
196	3.10	4.20	9.20	11.80	13.00	15.80
197	6.70	12.20	17.00	16.70	17.00	22.00
198	5.50	10.10	15.10	16.50	16.70	23.00
199	37.60	50.60	61.40	.	.	.
200	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
201	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
202	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
203	-9.00	-9.00	-9.00	-2.80	-2.80	-2.10
204	-1.50	2.80	3.70	4.10	5.70	5.50
205	2.90	-9.00	-9.00	-9.00	-9.00	-9.00
206	33.70	47.20	62.30	.	.	.
207	-9.00	-9.00	-9.00	-9.00	-9.00	-9.00
208	5.80	10.10	14.70	16.00	14.20	14.50

209	7.50	13.60	19.30	23.40	25.20	27.40
210	-1.10	1.80	2.20	5.10	6.50	7.10
211	4.90	10.10	12.10	12.20	12.00	10.60
212	1.90	6.50	9.50	11.20	15.80	16.00
213	21.80	31.40	42.20	.	.	.
214	-3.10	-1.50	.40	.50	2.00	2.70
215	-.50	-9.00	-9.00	-9.00	-2.60	-2.40
216	18.80	30.10	43.90	.	.	.

Columns 14 to 20

CASE NO	H9	R9	C9	W9	T9	RW9	N1
1	-9.000000
2	27.70	25.00	15.50	117.47	48.20	69.17	.0441
3	21.70	21.80	.	63.07	58.85	3.90	.0940
4	30.30	6.60	.	1.15	1.04	.12	.0102
5	25.20	20.10	12.60	58.41	25.47	32.94	.0096
60691
7	-9.000104
8	25.00	16.70	-98.00	56.45	30.42	35.98	.0044
9	21.10	11.50	.	83.28	78.41	4.67	.0415
10	19.50	15.40	.	2.32	1.79	.48	.0089
11	25.10	13.50	.	175.06	163.84	11.28	.0060
120099
13	19.00	18.60	.	51.71	48.43	3.09	.0062
14	10.60	15.30	.	1.19	.90	.26	.0050
150109
16	28.80	19.40	15.80	100.69	43.38	57.24	.0106
17	21.50	14.50	.	81.02	75.94	4.88	.0140
18	-9.000047
19	21.70	15.60	.	35.73	.	.	.0128
200296
21	19.60	15.00	.	77.45	71.83	5.44	.2084
22	19.90	7.00	.	.93	.83	.09	.0098
23	16.10	16.20	.	2.74	2.14	.54	.0124
24	-9.000000
25	-9.000000
26	25.10	21.00	15.70	118.57	58.21	60.26	.0116
27	-9.000000
28	21.50	16.90	.	34.16	.	.	.0053
29	-9.000000
30	-9.000000
310549
320158
33	20.30	18.10	.	15.64	.	.	.0051
34	25.80	16.30	13.00	66.25	27.95	38.33	.0141
35	26.90	20.70	14.90	87.77	36.39	51.41	.0048
36	23.80	6.70	.	.71	.60	.12	.0100
37	18.20	14.80	.	24.95	22.87	1.77	.0235
38	-9.000000
39	24.30	27.30	.	126.45	119.84	6.49	.0054
40	20.70	16.60	.	3.62	2.70	.90	.0076
41	-9.000000
42	25.60	17.40	16.80	122.96	46.79	76.20	.0202
43	24.50	15.40	.	187.27	179.78	7.64	.0073

440091
450088
46	-9.000000
47	22.00	19.60	.	31.61	25.50	5.26	.0169
48	21.80	16.80	.	115.59	108.37	6.69	.0194
49	-9.000000
50	21.00	16.10	.	8.22	5.78	2.43	.0392
51	38.30	6.00	.	2.13	1.93	.21	.0116
52	34.80	6.60	.	1.86	1.70	.18	.0058
53	-9.000000
54	25.50	19.30	.	171.06	160.91	9.60	.0426
55	28.60	5.30	.	.84	.69	.15	.0093
56	-9.000000
57	21.60	11.50	.	29.31	27.42	1.79	.2143
58	25.20	13.70	9.80	40.94	23.96	16.95	.0333
590390
60	30.30	10.70	.	1.05	.91	.15	.0127
61	23.20	13.70	.	164.90	156.08	8.64	.0245
62	-9.000000
63	24.50	13.70	.	72.35	68.32	3.75	.0264
64	23.90	22.20	.	32.90	26.4	5.80	.0533
65	26.50	15.00	.	29.19	.	.	.0378
660378
670182
68	26.50	22.60	13.20	62.49	24.90	37.56	.0154
69	-9.000096
70	22.40	17.70	.	141.11	133.24	7.96	.1074
71	21.70	14.50	.	171.77	159.08	12.62	.0082
720051
730055
74	18.70	21.00	.	94.68	86.84	7.61	.0266
750000
76	26.40	11.50	.	1.78	1.44	.34	.0119
77	33.10	6.60	.	3.93	3.58	.35	.0166
780000
790423
80	19.60	22.90	.	17.08	12.37	4.33	.0441
810387
82	20.30	18.80	.	16.06	12.07	3.30	.0523
83	21.60	13.10	.	107.95	101.93	5.99	.0079
84	29.30	10.10	.	2.99	2.36	.63	.0642
850000
86	26.20	10.60	.	1.13	.90	.23	.0664
87	20.80	22.20	146.4	1	137.56	8.81	.0189
880372
89	23.60	14.40	.	140.44	133.41	6.91	.0488
90	21.80	25.10	.	29.74	21.71	8.06	.0055
910075
92	27.00	18.70	12.90	86.49	52.62	35.77	.0103
930000
94	22.60	22.40	.	167.47	156.55	11.00	.0936
95	19.70	10.20	.	.51	.40	.12	.0142
960000
970000
980000
990080
1000000
101	17.90	13.50	.	82.62	78.81	3.84	.0199

1020288
1030155
104	20.90	8.60	.	1.17	.85	.32	.0116
105	23.50	13.50	.	66.17	63.27	2.83	.0142
106	24.00	15.90	.	22.27	17.17	4.66	.0084
107	23.90	16.00	.	8.43	5.84	2.55	.0157
108	24.70	13.70	8.80	29.42	17.84	11.56	.0178
109	24.10	10.50	.	1.17	.89	.28	.0107
110	30.10	14.00	16.20	99.58	33.37	66.18	.0094
111	28.30	16.40	14.00	90.98	40.20	50.75	.0112
1120319
113	25.40	10.50	.	136.16	130.30	5.90	.0124
114	25.90	13.70	.	182.17	172.82	9.37	.0126
1150000
1160288
117	31.20	12.80	.	2.55	2.00	.55	.0076
118	28.70	10.00	.	2.22	1.65	.58	.0090
1190000
120	28.10	14.80	12.90	64.61	32.07	32.54	.0141
121	24.80	21.90	.	265.42	248.27	17.15	.0406
122	24.50	17.10	.	19.72	16.92	2.82	.0103
123	26.10	20.20	.	6.75	5.36	1.40	.0107
124	25.20	16.20	.	41.44	36.98	4.59	.0125
1250000
126	24.50	13.20	.	192.85	183.66	9.30	.0096
127	21.00	11.10	.	49.71	46.79	2.88	.0112
128	37.60	12.30	.	3.48	2.84	.64	.0085
129	17.10	10.00	2.20	4.22	3.39	.81	.0088
130	20.30	12.00	.	5.33	3.56	1.78	.0098
131	18.40	17.50	.	2.35	1.70	.63	.0102
132	21.60	16.00	.	42.49	37.55	4.94	.0100
1330000
1340000
1350000
136	17.10	14.10	.	7.08	4.56	2.30	.0089
137	23.40	25.10	.	128.90	121.70	7.07	.0089
1380213
139	27.20	21.10	17.50	113.44	35.74	77.64	.0278
140	24.90	16.00	14.60	77.91	27.77	50.11	.0066
141	26.30	14.60	.	1.10	.84	.26	.0031
142	11.80	9.50	1.57	3.24	2.80	.45	.0237
143	24.10	17.50	12.90	73.59	27.34	46.24	.0056
1440050
1450000
146	37.00	10.50	.	4.10	3.43	.67	.0437
1470218
148	24.80	21.20	13.30	88.11	43.61	44.51	.0087
149	27.80	22.80	19.00	184.56	79.16	105.44	.0093
1500150
151	39.60	7.50	.	4.22	3.74	.48	.0466
152	18.60	17.00	.	12.30	9.24	2.99	.0068
153	12.30	14.30	.	2.46	1.74	.64	.0357
1540000
1550170
156	19.90	8.10	.	15.06	14.17	.77	.0110
157	32.70	6.60	.	1.10	1.00	.12	.0579
158	23.70	15.40	.	126.00	119.41	6.58	.0127
159	26.50	16.30	14.60	98.31	62.03	36.32	.0089

160	33.90	7.20	.	1.12	1.03	.10	.0580
161	29.60	14.20	12.90	80.19	42.08	38.16	.2832
162	24.70	25.50	.	157.13	148.36	8.78	.0095
1630000
164	20.70	11.70	.	3.19	2.65	.46	.0132
1650623
1660169
167	27.00	18.90	.	99.24	95.24	3.91	.0132
168	33.10	20.30	19.20	192.16	89.24	102.96	.0126
1690228
170	26.50	12.90	.	192.00	184.09	7.91	.0185
171	23.60	4.70	.	14.57	13.97	.57	.0181
172	25.90	17.20	.	96.39	91.75	4.64	.0115
173	29.10	13.80	.	69.86	67.01	2.83	.0135
1740000
175	18.10	7.60	.	1.03	.89	.11	.0150
1760148
177	26.80	12.70	.	39.12	37.18	1.92	.0115
178	24.90	19.00	.	60.92	57.53	3.36	.0083
179	28.10	24.10	.	50.49	39.60	8.75	.0076
180	26.30	16.70	.	51.96	50.02	2.49	.0106
181	23.80	8.00	.	1.54	1.24	.31	.0073
1820000
183	25.10	14.30	.	89.84	86.10	3.76	.0117
184	23.00	14.90	.	12.46	9.43	2.12	.0107
185	23.20	7.50	.	1.19	.94	.19	.0133
186	26.10	21.50	14.60	100.93	47.53	53.42	.0200
187	20.90	20.10	.	46.21	42.85	3.36	.0063
188	22.70	24.70	.	64.07	51.60	10.21	.0253
189	30.50	16.20	15.40	119.00	64.66	54.39	.1174
1900110
1910000
1920000
193	49.30	9.20	.	4.41	3.95	.46	.0210
1942228
195	31.50	13.90	.	2.40	1.92	.47	.0155
196	24.80	6.50	.	.44	.39	.04	.0135
197	25.20	25.40	.	183.80	174.13	9.65	.0183
198	25.10	19.70	.	234.83	223.67	11.12	.0337
1990186
2000000
2010000
2020000
203	7.40	-98.00	.	.33	.28	.06	.0091
204	13.60	5.20	.63	1.60	1.53	.07	.0106
2050118
2060135
2070000
208	28.50	16.00	.	184.01	176.39	7.60	.0075
209	30.60	18.60	21.20	246.68	87.21	159.52	.0055
210	18.60	20.90	.	5.79	4.19	1.46	.0114
211	19.60	27.50	.	36.97	24.95	11.07	.1142
212	24.00	-98.00	.	117.10	111.05	6.07	.0062
2130041
214	10.30	6.40	.	.10	.05	.04	.0027
215	6.60	6.90	.	.31	.22	.11	.0030
2160265

Columns 21 to 27

CASE_	N2	N3	N4	N5	N6	AHGR2	AHGR3
NO							
1	.0000	.0000	.0000	.0000	.0000	.	.
2	.0078	.0073	.0818	.0171	.0127	.23	.70
3	.0864	.0089	.0060	.0289	.0242	.19	.49
4	.0301	.0078	.0211	.0117	.0118	.	.49
5	.0153	.0352	.0170	.0338	.0187	.23	.66
6	.0282	.0153	.0267	.0173	.0195	1.83	2.21
7	.0320	.0113	.0840	.0761	.0341	.	.
8	.0132	.0173	.0156	.0130	.0229	.11	.71
9	.0208	.0126	.0305	.0305	.0051	.30	.66
10	.0420	.0117	.0467	.1447	.0444	-.09	.23
11	.0381	.0533	.2051	.0321	.0042	.40	.44
12	.0264	.1383	.0346	.0257	.0273	1.73	1.33
13	.0269	.0584	.0054	.0408	.2045	.30	.34
14	.0230	.0076	.0080	.0089	.0053	.	.
15	.0133	.0408	.0158	.0275	.0148	1.39	2.13
16	.0093	.0255	.0251	.0141	.0096	.17	.89
17	.0299	.0176	.0066	.0259	.0161	.10	.53
18	.0120	.0144	.0163	.0144	.0123	-.04	.
19	.0119	.0129	.0141	.0570	.0137	.56	.20
20	.0147	.0305	.0193	.0200	.0372	.97	1.84
21	.0181	.0210	.0153	.0514	.0045	.43	.56
22	.0175	.0202	.0139	.0465	.2044	.14	.80
23	.1172	.0096	.0081	.0244	.0096	.01	.07
24	.0000	.0000	.0000	.0000	.0000	.	.
25	.0000	.0000	.0000	.0000	.0000	.	.
26	.0227	.1086	.0072	.0346	.0078	.21	.71
27	.0000	.0000	.0000	.0000	.0000	.	.
28	.0296	.0902	.0188	.0110	.0079	.24	.37
29	.0000	.0000	.0000	.0000	.0000	.	.
30	.0000	.0000	.0000	.0000	.0000	.	.
31	.0177	.0160	.0269	.0179	.0117	1.57	2.00
32	.2324	.0205	.0078	.0159	.0073	1.19	1.43
33	.1298	.0904	.0345	.0104	.0091	.17	.27
34	.0255	.0168	.0073	.2161	.0063	.26	.54
35	.0045	.1620	.0563	.0096	.0098	.24	.51
36	.0275	.0148	.0217	.0590	.0087	.	1.11
37	.0145	.0178	.0076	.0353	.0084	.07	.26
38	.0000	.0000	.0000	.0000	.0000	.	.
39	.0547	.0590	.0074	.0122	.0189	.23	.51
40	.0127	.0196	.0251	.0482	.0354	-.04	.34
41	.0000	.0000	.0000	.0000	.0000	.	.
42	.0132	.0148	.0112	.0235	.0065	.21	1.00
43	.0118	.0471	.0270	.0270	.0041	.34	.54
44	.0102	.0550	.0200	.0086	.0250	1.59	2.09
45	.0159	.0134	.0056	.0110	.0046	1.26	1.44
46	.0000	.0000	.0000	.0000	.0000	.	.
47	.0110	.0105	.0094	.0178	.0116	.11	.24
48	.0109	.0186	.0105	.0123	.0135	.20	.43
49	.0000	.0000	.0000	.0000	.0000	.	.
50	.0101	.0131	.0224	.0160	.0109	-.03	.33
51	.0091	.0482	.0214	.0248	.0115	.07	1.20
52	.0279	.0114	.0239	.0079	.0223	.06	1.17
53	.0000	.0000	.0000	.0000	.0000	.	.

54	.0097	.0360	.0464	.0254	.0032	.46	.69
55	.0102	.0228	.0094	.0181	.0122	.	.96
56	.0000	.0000	.0000	.0000	.0000	.	.
57	.0098	.0421	.0079	.0480	.0436	.14	.30
58	.0033	.0125	.0317	.0089	.2584	.17	.51
59	.0083	.1407	.0337	.0326	.0126	1.46	2.14
60	.0112	.0563	.2076	.0543	.0284	.33	1.03
61	.2531	.0115	.0322	.0087	.0098	.31	.61
62	.0000	.0000	.0000	.0000	.0000	.	.
63	.0225	.0198	.0160	.0145	.0277	.23	.61
64	.0203	.0116	.0278	.0467	.0199	.24	.70
65	.0082	.0132	.0305	.1546	.0109	.24	.29
66	.0092	.0388	.0286	.0355	.0104	1.36	1.70
67	.5031	.0318	.0105	.0167	.0074	1.69	2.10
68	.0029	.0232	.0090	.5162	.0064	.33	.71
69	.0078	.0245	.1181	.0221	.0108	.	.
70	.0069	.0152	.0131	.0161	.0103	.39	.43
71	.0073	.0058	.0107	.0055	.0086	.13	.54
72	.0077	.0061	.0045	.0099	.0029	.81	1.14
73	.0027	.0048	.0107	.0106	.0034	1.34	1.57
74	.0023	.0366	.0040	.0096	.0048	.17	.43
75	.0000	.0000	.0000	.0000	.0000	.	.
76	.0038	.0079	.0057	.0728	.0098	.17	1.01
77	.0031	.0274	.0044	.0166	.0189	.39	.97
78	.0000	.0000	.0000	.0000	.0000	.	.
79	.0045	.0070	.0095	.0880	.0087	1.80	2.71
80	.0030	.2026	.0064	.0165	.0269	-.19	.20
81	.0056	.0080	.0085	.0886	.0126	2.27	2.01
82	.0029	.2025	.0076	.0164	.0235	.16	.37
83	.0049	.0089	.0020	.0321	.0053	.36	.49
84	.0026	.0300	.0139	.0120	.0128	.19	1.30
85	.0000	.0000	.0000	.0000	.0000	.	.
86	.0031	.0337	.0271	.0198	.0149	.23	.80
87	.0099	.0108	.0068	.0291	.0084	.34	.61
88	.0046	.0202	.0128	.0111	.0270	1.37	1.86
89	.0034	.0129	.0023	.0174	.0171	.40	.53
90	.0073	.0047	.0079	.0289	.0052	.37	.34
91	.0187	.0212	.0088	.0220	.0080	1.30	2.60
92	.0046	.0109	.0088	.0426	.0143	.26	.91
93	.0000	.0000	.0000	.0000	.0000	.	.
94	.0052	.0102	.0140	.0285	.0101	.33	.67
95	.0062	.0096	.0106	.0275	.0894	.	.47
96	.0000	.0000	.0000	.0000	.0000	.	.
97	.0000	.0000	.0000	.0000	.0000	.	.
98	.0188	.0141	.0109	.0237	.0099	1.84	2.43
99	.0000	.0000	.0000	.0000	.0000	.	.
100	.0157	.0147	.0722	.0202	.0285	1.37	2.20
101	.0122	.0125	.0341	.0434	.0105	.30	.53
102	.0078	.0093	.0097	.0144	.0231	.64	3.30
103	.0192	.0199	.0264	.0769	.0351	.00	.
104	.0061	.0080	.0054	.0220	.0110	.	.27
105	.0527	.0761	.0261	.0261	.0198	.40	.43
106	.0554	.0130	.0116	.0137	.0135	.13	.39
107	.5179	.0146	.0744	.0195	.0246	.01	.39
108	.0172	.5139	.0493	.0193	.0263	.16	.67
109	.0199	.0185	.0139	.0364	.0181	.23	.87
110	.0329	.0460	.0077	.0101	.0164	.21	.91
111	.0369	.0279	.0089	.0105	.0478	.14	.90

112	.0160	.0162	.0067	.0222	.0152	1.57	2.69
113	.0506	.0288	.0100	.0127	.0363	.37	.66
114	.0346	.0257	.0063	.0098	.0365	.40	.53
115	.0000	.0000	.0000	.0000	.0000	.	.
116	.0260	.0217	.0040	.0197	.0194	1.84	2.19
117	.0137	.0222	.0030	.0290	.0448	.41	.96
118	.0134	.0110	.0037	.0059	.0112	.21	.99
119	.0000	.0000	.0000	.0000	.0000	.	.
120	.0143	.0354	.0039	.0271	.0212	.23	.86
121	.0129	.0352	.0025	.0152	.0141	.39	.54
122	.0289	.1132	.0051	.0109	.0343	.27	.06
123	.0246	.1115	.0056	.0093	.0422	-.49	.51
124	.0209	.0644	.0027	.0137	.2173	.39	.50
125	.0000	.0000	.0000	.0000	.0000	.	.
126	.0400	.0592	.0077	.0087	.0096	.43	.53
127	.0192	.3171	.0025	.0130	.0145	.20	.34
128	.0110	.0098	.0055	.0061	.0080	.56	1.00
129	.0175	.0449	.0057	.0106	.0354	.16	.30
130	.0153	.0794	.0021	.0105	.0465	.	.34
131	.0208	.0887	.0024	.0154	.0722	.	.09
132	.0322	.0329	.0037	.0246	.0170	.23	.47
133	.0000	.0000	.0000	.0000	.0000	.	.
134	.0000	.0000	.0000	.0000	.0000	.	.
135	.0000	.0000	.0000	.0000	.0000	.	.
136	.0218	.0397	.0017	.0093	.0127	.01	.34
137	.0260	.0133	.0011	.0079	.0106	.29	.41
138	.0403	.0468	.0027	.0041	.0110	1.21	1.36
139	.0126	.0351	.0018	.0170	.0081	.50	1.04
140	.0180	.0123	.0097	.0079	.0067	.16	.67
141	.0521	.0204	.0020	.0203	.0063	.	.67
142	.0182	.0182	.0028	.0188	.0064	.24	.16
143	.0104	.0064	.0075	.0230	.0043	.24	.76
144	.0262	.0049	.0039	.0024	.0034	1.41	1.37
145	.0000	.0000	.0000	.0000	.0000	.	.
146	.0077	.0121	.0066	.0174	.0074	.	.91
147	.0184	.0362	.0065	.0409	.0063	1.17	2.53
148	1.0070	.0308	.0064	.0264	.0048	.29	.41
149	1.0070	.0263	.0065	.0323	.0049	.21	.93
150	.0428	.0234	.0071	.0408	.0061	1.01	1.84
151	.0101	.0201	.0087	.0225	.0100	.11	1.20
152	.0486	.0073	.0066	.0121	.0044	.16	.06
153	.0166	.0073	.0087	.0527	.0089	-.03	-.01
154	.0000	.0000	.0000	.0000	.0000	.	.
155	.0094	.0091	.0465	.0101	.0712	1.69	2.04
156	.0067	.0076	.0071	.0463	.0902	.83	-.50
157	.0370	.0200	.0191	.0385	.0188	.	.94
158	.0088	.0092	.0651	.0598	.0650	.31	.74
159	.0195	.0276	.0213	.0111	.0071	.16	.39
160	.2593	.0177	.0202	.0620	.0250	.16	1.04
161	.0084	.0165	.0201	.0523	.0261	.24	1.23
162	.0072	.0091	.0379	.0222	.0655	.31	.54
163	.0000	.0000	.0000	.0000	.0000	.	.
164	.0751	.0121	.1760	.0178	.0137	.07	-.01
165	.0393	.0214	.0295	.0523	.0475	1.61	2.19
166	.0392	.0740	.0581	.0265	.0236	.10	.
167	.2179	.1239	.0566	.0195	.0155	.19	.47
168	.0175	.0616	.2282	.0167	.0127	.19	.96
169	.0192	.0385	.0430	.0574	.1783	1.41	2.40

170	.0192	.0747	.0398	.0934	.0299	.47	.57
171	.0166	.0369	.0693	.1625	.0395	.39	.37
172	.0114	.0247	.0821	.0224	.0282	.44	.69
173	.0136	.0264	.0656	.0364	.0924	.43	.56
174	.0000	.0000	.0000	.0000	.0000	.	.
175	.0164	.0150	.0376	.1389	.0926	.11	.50
176	.0174	.1151	.0324	.0233	.0541	1.49	2.30
177	.0139	.0336	.1039	.0264	.0534	.34	.53
178	.0096	.2202	.0362	.0149	.0392	.29	.50
179	.0089	.0190	.2260	.0138	.0323	.41	.60
180	.0160	.0502	.0804	.0195	.0659	.37	.67
181	.0123	.0150	.0114	.0113	.0083	.	.26
182	.0000	.0000	.0000	.0000	.0000	.	.
183	.0288	.1758	.0685	.0187	.0185	.27	.61
184	.0207	.0738	.0373	.0199	.0693	.16	.21
185	.0507	.0712	.0348	.0201	.1282	.	.14
186	.0190	.0633	.0207	.0232	.0341	.19	.63
187	.0074	.0175	.0116	.0200	.0127	.79	-.31
188	.0100	.0081	.0066	.0096	.0064	.00	.29
189	.0192	.0200	.0113	.0701	.0155	.20	.97
190	.0119	.0210	.0108	.0132	.0349	1.27	1.81
191	.0000	.0000	.0000	.0000	.0000	.	.
192	.0000	.0000	.0000	.0000	.0000	.	.
193	.1137	.0179	.0096	.2107	.0141	.	1.37
194	.0735	.0177	.0096	.0117	.0161	1.34	2.49
195	.0139	.0237	.0069	.0142	.0076	.20	.84
196	.0208	.0166	.0091	.0359	.0446	.	.60
197	.0146	.0138	.0079	.0712	.0233	.50	.57
198	.0200	.0149	.0086	.0569	.0209	.36	.64
199	.0190	.0137	.0078	.0172	.0959	1.67	1.90
200	.0000	.0000	.0000	.0000	.0000	.	.
201	.0000	.0000	.0000	.0000	.0000	.	.
202	.0000	.0000	.0000	.0000	.0000	.	.
203	.0209	.0103	.0159	.0133	.0069	-.04	.
204	.0182	.0295	.0178	.0327	.0132	.09	.13
205	.0163	.0243	.0080	.1395	.0114	.29	.41
206	.1480	.0330	.0099	.0134	.0100	1.24	2.54
207	.0000	.0000	.0000	.0000	.0000	.	.
208	.0241	.0351	.0520	.0145	.0060	.39	.46
209	.0061	.0216	.0211	.0254	.0041	.20	.86
210	.0278	.0150	.0331	.0219	.0063	.01	-.04
211	.0197	.0124	.0073	.0344	.0055	.47	.17
212	.0204	.0233	.0517	.0129	.0045	.23	.30
213	.0233	.0191	.0091	.0044	.0030	1.36	1.17
214	.0134	.1223	.0070	.0378	.0046	.	-.01
215	.0062	.0049	.0042	.0134	.0022	.19	-.07
216	.0074	.0197	.0046	.0072	.0035	.97	1.11

Columns 28 to 33

CASE_	AHGR4	AHGR5	AHGR6	AHGR7	AHGR8	AHGR9
NO						
1
2	1.10	.71	.23	.49	.03	-.05
3	.71	.39	.22	.24	.06	.13
4	.44	.16	.66	1.17	.00	.27
5	.97	.54	.32	.57	-.03	-.06
6	1.77	1.93
7
8	.79	.59	.16	.70	.00	-.02
9	.83	.36	.19	.19	-.01	.06
10	.36	.39	.36	.34	.03	.24
11	.64	.56	.34	.47	-.07	.12
12	1.86	1.54
13	.63	.46	.37	.14	-.03	.05
14	.21	.09	.26	.10	.09	.32
15	1.90	1.99
16	1.04	.80	.26	3.33	-2.77	-.06
17	.77	.41	.20	.29	-.09	.13
18
19	.57	.03	.27	.13	.03	.13
20	2.40	1.49
21	.49	.93	.04	-.20	.19	.04
22	.10	.14	-.05	.26	-.13	.34
23	.21	.24	.13	.49	.19	.27
24
25
26	.94	.63	.14	.54	.01	-.06
27
28	.53	.27	.09	.26	.03	.18
29
30
31	1.61	1.40
32	2.19	1.49
33	.74	-.01	.35	-.06	.10	.19
34	1.24	.54	.16	.20	.06	.01
35	.81	.76	.45	.47	-.17	.07
36	.51	.23	.05	.06	.33	.16
37	.34	.49	.09	.44	.14	.23
38
39	.53	.63	.25	.31	-.19	.28
40	.34	.61	.33	.30	.01	.24
41
42	1.13	.47	.13	.00	.16	-.11
43	.53	.97	.27	.01	.29	.04
44	1.94	1.54
45	2.01	1.24
46
47	.43	.71	.14	.33	-.10	.19
48	.53	.80	.16	.37	-.09	.11
49
50	.46	.39	.29	.61	-.10	.30
51	.41	.10	.64	.37	.10	.74

52	.66	.10	.57	.76	.01	.37
53
54	.84	.63	.13	-.04	.23	.09
55	.33	.01	.36	.86	.04	.36
56
57	.96	.43	.14	-.09	.19	.25
58	.71	.71	.48	.60	-.03	.00
59	2.26	1.66
60	.27	.16	.38	.10	.01	.57
61	.74	.43	.31	.23	.10	.06
62
63	.49	.83	.14	.66	.01	.05
64	.97	.00	.36	-.03	-.01	.10
65	.74	.56	.14	.40	.01	.18
66	1.49	1.51
67	1.90	1.71
68	1.21	.49	-.17	.37	.07	.05
69
70	.60	.49	.24	.34	-.17	.18
71	.53	.63	.24	.39	.04	.05
72	1.41	1.60
73	1.91	1.26
74	.51	.36	.27	.19	.07	.19
75
76	.26	.07	.05	.37	.27	.40
77	.36	.79	.09	.17	.20	.45
78
79	1.83	1.03
80	.47	.21	.04	.83	.06	.16
81	1.86	1.74
82	.30	.40	.05	.74	-.01	.22
83	.57	.30	.19	.01	-.04	.26
84	.16	-.01	.56	.20	.14	.25
85
86	.10	.37	.37	.41	-.01	.38
87	.69	.46	.07	-.01	.11	.14
88	1.84	1.96
89	.44	.46	.25	-.01	-.07	.34
90	.41	.16	.	.	.06	.15
91	2.09	1.36
92	.79	.81	.14	.19	.03	.06
93
94	.57	.70	.04	.11	.00	.16
95	.50	.20	.00	.41	.31	.13
96
97
98	1.96	1.83
99
100	2.36	2.01
101	.63	.54	.08	.10	-.03	.06
102	2.13	1.91
103
104	.34	.47	.13	.43	.37	.22
105	.80	.46	.09	.07	.10	.19
106	.89	.39	.31	.17	-.14	.22
107	.29	.34	.33	.34	.53	.32
108	.69	.61	.27	.47	.20	.02
109	-.14	.46	.20	.10	.39	.26

110	1.37	.54	.23	.59	.00	-.07
111	.96	.90	.21	.29	.04	-.01
112	2.24	2.40
113	.59	.87	.10	.11	-.10	.25
114	.80	.61	.10	.19	-.17	.29
115
116	1.99	2.13
117	.16	.86	.23	.30	.04	.27
118	.13	.84	.31	.04	.03	.32
119
120	.87	.73	.09	.44	.11	.03
121	.57	.63	.09	.37	-.04	.21
122	.30	.90	.29	.29	.10	.23
123	.36	.31	.61	.36	.13	.41
124	.89	.21	.05	.94	-.71	.21
125
126	.77	.47	.27	.19	.19	.08
127	.67	.61	.36	.30	.17	.02
128	.19	.60	.42	.39	.24	.49
129	.69	.44	.09	.43	-.01	.08
130	.50	.34	.14	.51	.03	.34
131	.10	.33	.21	.53	-.04	.40
132	.51	.47	.15	-.06	.00	.23
133
134
135
136	.34	.36	.15	.21	.00	.27
137	.69	.61	.25	.20	.00	.18
138	1.69	1.93
139	.90	.74	-.04	.14	-.04	-.03
140	.56	1.17	.35	.09	-.04	.04
141	.39	.13	.23	.51	.03	.46
142	2.74	-1.86	.07	.03	-.04	.15
143	.60	.83	.13	.51	-.03	-.10
144	1.51	1.74
145
146	.74	.06	.19	.56	.81	.46
147	1.19	1.63
148	.59	.79	.39	.51	.06	.04
149	.50	1.29	.31	.19	-.03	-.06
150	1.23	1.17
151	.20	.87	.25	.27	.43	.56
152	.27	.41	.11	.19	.04	.38
153	-.01	.27	.08	.09	.13	.29
154
155	1.36	1.29
156	.33	.29	.10	.63	.19	.31
157	.30	.10	.14	.57	.43	.55
158	.89	.31	.14	.20	-.03	.18
159	.67	.84	.34	.73	.14	.03
160	.40	-.01	.46	.00	.06	.75
161	.39	.71	.31	.40	.17	.02
162	.74	.54	.20	.11	.16	.19
163
164	.33	.29	.28	.51	.16	.37
165	1.99	2.10
166
167	.59	.53	.35	.47	.06	.22

168	.57	1.13	.15	.73	.17	.07
169	2.46	2.54
170	.84	.66	.01	.27	-.01	.16
171	.77	.14	.17	.21	.	.
172	.93	.31	.26	.30	.04	.09
173	.74	.67	.21	.07	.00	.34
174
175	.24	.01	.01	-.20	.40	.34
176	2.09	1.99
177	.80	.76	.11	.01	-.01	.27
178	.69	.61	.15	.43	-.16	.19
179	.71	.80	.19	.01	.31	.08
180	.57	.66	.16	.07	-.10	.31
181	.33	.07	.38	.51	.21	.38
182
183	.89	.51	.13	.41	-.21	.20
184	.24	.41	.26	.41	.00	.28
185	.07	.36	.09	.71	.20	.57
186	1.06	.63	.04	.66	.06	-.01
187	.60	.20	.26	.53	.03	.25
188	.34	.50	.13	.27	.16	.34
189	.64	.87	.02	.47	.21	.17
190	2.31	1.80
191
192
193	.11	.39	.49	.27	1.19	.73
194	1.87	1.94
195	.27	.04	.25	.49	.81	.40
196	.16	.71	.33	.17	.40	.25
197	.79	.69	-.04	.04	.00	.21
198	.66	.71	.17	.03	.20	.15
199	1.86	1.54
200
201
202
20300	.10	.28
204	.61	.13	.05	.23	-.03	.21
205
206	1.93	2.16
207
208	.61	.66	.16	-.26	.04	.51
209	.87	.81	.51	.26	.31	-.05
210	.41	.06	.36	.20	.09	.38
211	.74	.29	.01	-.03	-.20	.25
212	.66	.43	.21	.66	.03	.19
213	1.37	1.54
214	.23	.27	.01	.21	.10	.18
21503	.26
216	1.61	1.97

Part 3 Programs

```
*** PLC1ANL31.INC: analysis of results from yr 3 expt 1 ***.
SET ECHO ON.
SET MORE OFF.
GET FILE = 'ldata.sys'
  /DROP = mySample pos countOrd.
SELECT IF ((rep GT 0)
            AND (treat = 1 OR treat = 2)
            AND (recDon = 1 OR recDon = 2)
            AND (rtSht = 1 OR rtSht = 2)).
COMPUTE CPMperg = cpm3 / wtCountd.
VARIABLE LABEL CPMperg '3rd counts per minute per g d.wt.'.
SORT CASES BY rep treat potNo.
COMPUTE spDon = 0.
COMPUTE donRtCPG = 0.
COMPUTE recRtCPG = 0.
COMPUTE relRtCPG = 0.
COMPUTE re2RtCPG = 0.
COMPUTE re3RtCPG = 0.
COMPUTE donShDW = 0.
COMPUTE relShDW = 0.
COMPUTE re2ShDW = 0.
COMPUTE re3ShDW = 0.
COMPUTE shDW = 0.
COMPUTE rtDW = 0.
IF (plantID = 3 AND recDon = 1) spDon = 2.
IF ((plantID = 1 OR plantID = 2) AND recDon = 1) spDon = 1.
IF (recDon = 2 AND rtSht = 1) recRtCPG = CPMperg.
IF (recDon = 1 AND rtSht = 1) donRtCPG = CPMperg.
IF (recDon = 2 AND rtSht = 1 AND plantID = 1) relRtCPG =
CPMperg.
IF (recDon = 2 AND rtSht = 1 AND plantID = 2) re2RtCPG =
CPMperg.
IF (recDon = 2 AND rtSht = 1 AND plantID = 3) re3RtCPG =
CPMperg.
IF (recDon = 1 AND rtSht = 2) donShDW = DW.
IF (recDon = 2 AND rtSht = 2 AND plantID = 1) relShDW = DW.
IF (recDon = 2 AND rtSht = 2 AND plantID = 2) re2ShDW = DW.
IF (recDon = 2 AND rtSht = 2 AND plantID = 3) re3ShDW = DW.
IF (rtSht = 1) rtDW = DW.
IF (rtSht = 2) shDW = DW.
AGGREGATE OUTFILE = *
  /BREAK = rep treat potNo
  /spDon      = MAX (spDon)
  /donRtCPG   = MAX (donRtCPG)
  /relRtCPG   = MAX (relRtCPG)
  /re2RtCPG   = MAX (re2RtCPG)
  /re3RtCPG   = MAX (re3RtCPG)
  /donShDW    = MAX (donShDW)
  /relShDW    = MAX (relShDW)
  /re2ShDW    = MAX (re2ShDW)
  /re3ShDW    = MAX (re3ShDW)
  /potShDW    = SUM (shDW)
  /potRtDW    = SUM (rtDW).
COMPUTE potTotDW = potShDW + potRtDW.
COMPUTE C14TrL1 = 0.
COMPUTE C14TrL2 = 0.
COMPUTE C14LpTr = 0.
```



```

IF (spDon = 2) C14TrL1 = donRtCPG / re1RtCPG.
IF (spDon = 2) C14TrL2 = donRtCPG / re2RtCPG.
IF (spDon = 1) C14LpTr = donRtCPG / re3RtCPG.
COMPUTE DWTrL1 = 0.
COMPUTE DWTrL2 = 0.
COMPUTE DWLpTr = 0.
IF (spDon = 2) DWTrL1 = donShDW / re1ShDW.
IF (spDon = 2) DWTrL2 = donShDW / re2ShDW.
IF (spDon = 1) DWLpTr = donShDW / re3ShDW.
MIS VAL ALL (0).
VARIABLE LABELS
  /spDon      'Donor species'
  /C14TrL1    'Tr Don/L1: rt CPM/g ratio'
  /C14TrL2    'Tr Don/L2: rt CPM/g ratio'
  /C14LpTr    'Lp Don/Tr: rt CPM/g ratio'
  /DWTrL1     'Tr Don/L1: Sh DW ratio'
  /DWTrL2     'Tr Don/L2: Sh DW ratio'
  /DWLpTr     'Lp Don/Tr: Sh DW ratio'
  /donRtCPG   'Donor rt CPM/g'
  /re1RtCPG   'Recvr 1 root CPM/g'
  /re2RtCPG   'Recvr 2 rt CPM/g'
  /re3RtCPG   'Recvr 3 rt CPM/g'
  /potTotDW   'Pot tot sht + rt DW'
  /potShDW    'Pot tot shoot DW'
  /potRtDW    'Pot tot root DW'.
VALUE LABELS spDon 1 'L. perenne' 2 'T.repens'.
FORMATS donRtCPG TO re3RtCPG (F9.0)
        C14TrL1 TO DWLpTr (F5.4).
*****
**.
*** Now put C14LpTr, C14TrL1 & C14TrL2 values -> 3 recs, same
var.
SORT CASES BY spDon treat.
SAVE OUTFILE = 'potrecs.tmp'
  /COMPRESSED.
GET FILE = 'potrecs.tmp'.
COMPUTE c14ratio = 0.
COMPUTE DWratio = 0.
SELECT IF (spDon = 1).
COMPUTE c14ratio = C14LpTr.
COMPUTE DWratio = DWLpTr.
COMPUTE recvrID = 3.
SAVE OUTFILE = 'recv3.tmp'
  /COMPRESSED.
GET FILE = 'potrecs.tmp'.
COMPUTE c14ratio = 0.
COMPUTE DWratio = 0.
SELECT IF (spDon = 2).
COMPUTE c14ratio = C14TrL1.
COMPUTE DWratio = DWTrL1.
COMPUTE recvrID = 1.
SAVE OUTFILE = 'recv1.tmp'
  /COMPRESSED.
GET FILE = 'potrecs.tmp'.
COMPUTE c14ratio = 0.
COMPUTE DWratio = 0.
SELECT IF (spDon = 2).
COMPUTE c14ratio = C14TrL2.
COMPUTE DWratio = DWTrL2.
COMPUTE recvrID = 2.

```

```

SAVE OUTFILE = 'recv2.tmp'
/COMPRESSED.
JOIN ADD
/FILE = 'recv1.tmp'
/FILE = 'recv2.tmp'
/FILE = 'recv3.tmp'.
VARIABLE LABELS C14Ratio 'Don/Recv (CPM per g DW root)'
/DWRatio 'Don/Recv (Shoot Dry Wts)'
/recvrID 'ID of receiver concerned'.
VALUE LABELS recvrID 1 'Lp1' 2 'Lp2' 3 'Tr'.
MISSING VALUE ALL 0.
MISSING VALUE C14ratio (-9).
SAVE OUTFILE = 'ratio.sys'
/DROP = relRtCPG TO DWLpTr
/COMPRESSED.
GET FILE = 'ratio.sys'.
SORT CASES BY spDon treat.
SET LENGTH 66.
SET LISTING = 'plclan11.lis'.
*** Use only cases where donor's roots have a reasonably high
CPM.
*** (indicates that the feeding of CO2 was successful).
*** and remove the one with only 0.003g root.
IF ((potNo = 98 AND recvrID = 1) OR donRtCPG < 30000) C14ratio =
-9.
ANOVA VARIABLES = C14ratio
BY treat (1, 2) spDon (1, 2).
MEANS TABLES = C14ratio BY treat BY spdon.

```

Part 3 Data

MYSAMPLE	-	no. on drying tray and counting vial
POS	-	position in counter
CPM	-	Counts Per Minute
RTSHT	-	whether root or shoot
RECDON	-	whether receiver, donor or control
WTCOUNTD	-	D.Wt. in counting vial (g)
REP	-	replicate
PLANTID	-	Lp1 or Lp2 or Tr
POTNO	-	pot number
TREAT	-	treatment
FW	-	fresh weight (g)
DW	-	dry weight (g)

```
Variable: RTSHT      Label: whether root or shoot
Value labels follow  Type: Number  Width: 1  Dec: 0
Missing: * None *
      1.00    root
      2.00    shoot
```

Variable: RECDON	Label: whether receiver, donor or control
Value labels follow	Type: Number Width: 1 Dec: 0
Missing: * None *	
1.00 donor	2.00 receiver
3.00 unfed pot	4.00 hot leaf

```

      Value labels follow   Type: Number   Width:  3   Dec: 0
Missing: * None *
      .00   unfed

```

```
Variable: PLANTID      Label: Lp1 or Lp2 or Tr
Value labels follow    Type: Number  Width: 1  Dec: 0
Missing: * None *
      1.00    L.p.1
      3.00    T. repens      2.00    L.p.2
```

```
Variable: TREAT      Label: treatment
Value labels follow  Type: Number  Width:  1  Dec:  0
Missing: * None *
      2.00    familiar      1.00    alien
```

Radiation counts

\$CASE NUM	MYSAM PLE	POS	CPM	RTSHT	RECDO N	WTCOU NTD	REP
1	1	180	115.20	2	2	.036	0
68	1	247	721.20	1	2	.048	0
2	2	181	232.90	2	2	.043	0
69	2	248	937.20	1	2	.051	0
3	3	182	79.80	2	2	.050	0
70	3	249	51.30	1	2	.046	0
133	4	13	606.70	1	1	.047	1
166	4	46	262.60	2	1	.044	1
4	5	183	367.60	2	2	.040	1
71	5	250	422.30	1	2	.050	1
5	6	184	96.40	2	2	.049	1
72	6	251	36.90	1	2	.044	1

134	7	14	590.30	1	1	.049	1
167	7	47	226.10	2	1	.049	1
6	8	185	307.50	2	2	.039	1
73	8	252	947.70	1	2	.047	1
7	9	186	77.00	2	2	.042	1
74	9	253	51.60	1	2	.050	1
135	10	15	42.60	1	1	.054	2
168	10	48	35.40	2	1	.048	2
8	11	187	342.90	2	2	.037	2
75	11	254	492.50	1	2	.046	2
9	12	188	329.30	2	2	.043	2
76	12	255	383.70	1	2	.050	2
136	13	16	41.50	1	1	.050	2
169	13	49	33.60	2	1	.052	2
10	14	189	269.00	2	2	.023	2
77	14	256	272.40	1	2	.046	2
11	15	190	283.00	2	2	.051	2
78	15	257	237.10	1	2	.048	2
137	16	17	2808.10	1	1	.050	3
170	16	50	13110.40	2	1	.039	3
12	17	191	411.10	2	2	.047	3
79	17	258	681.80	1	2	.045	3
13	18	192	83.60	2	2	.041	3
80	18	259	291.80	1	2	.050	3
138	19	18	472.10	1	1	.040	3
171	19	51	186.20	2	1	.031	3
14	20	193	250.10	2	2	.037	3
81	20	260	1055.10	1	2	.039	3
15	21	194	87.40	2	2	.049	3
82	21	261	22.20	1	2	.049	3
139	22	19	45.70	1	1	.048	4
172	22	52	34.80	2	1	.052	4
16	23	195	248.20	2	2	.043	4
83	23	262	391.00	1	2	.050	4
17	24	196	354.90	2	2	.041	4
84	24	263	637.90	1	2	.049	4
18	25	197	397.10	2	2	.041	4
85	25	264	1131.70	1	2	.046	4
19	26	198	222.70	2	2	.049	4
86	26	265	762.00	1	2	.049	4
140	27	20	73.60	1	1	.014	4
173	27	53	43.80	2	1	.041	4
20	28	199	140.40	2	2	.042	5
87	28	266	1980.80	1	2	.056	5
21	29	200	301.40	2	2	.019	5
141	30	21	7521.60	1	1	.040	5
174	30	54	5416.80	2	1	.040	5
22	31	201	76.20	2	2	.036	5
88	31	267	153.80	1	2	.053	5
23	32	202	342.00	2	2	.042	5
89	32	268	952.30	1	2	.050	5
142	33	22	1746.20	1	1	.040	5
175	33	55	777.50	2	1	.043	5
24	34	203	455.70	2	2	.044	6
90	34	269	356.50	1	2	.048	6
25	35	204	447.00	2	2	.019	6
91	35	270	601.00	1	2	.046	6
143	36	23	2668.00	1	1	.044	6

176	36	56	1318.20	2	1	.048	6
26	37	205	249.40	2	2	.030	6
92	37	271	785.90	1	2	.046	6
27	38	206	242.50	2	2	.043	6
93	38	272	990.40	1	2	.046	6
144	39	24	675.70	1	1	.046	6
177	39	57	174.60	2	1	.040	6
28	40	207	245.50	2	2	.018	7
94	40	273	427.60	1	2	.026	7
29	41	208	78.90	2	2	.043	7
95	41	274	82.60	1	2	.052	7
145	42	25	724.70	1	1	.050	7
178	42	58	899.60	2	1	.038	7
30	43	209	79.80	2	2	.050	7
96	43	275	208.00	1	2	.050	7
31	44	210	300.40	2	2	.025	7
97	44	276	694.80	1	2	.040	7
146	45	26	952.90	1	1	.038	7
179	45	59	604.30	2	1	.031	7
32	46	211	301.20	2	2	.044	8
147	46	27	953.60	1	1	.046	8
33	47	212	284.90	2	2	.044	8
98	47	277	1271.91	1	2	.047	8
148	48	28	854.40	1	1	.046	8
180	48	60	306.10	2	1	.055	8
34	49	213	407.90	2	2	.043	8
99	49	278	841.00	1	2	.052	8
35	50	214	369.60	2	2	.036	8
100	50	279	937.00	1	2	.047	8
149	51	29	1980.80	1	1	.043	8
181	51	61	93.70	2	1	.048	8
36	52	215	75.60	2	2	.050	9
101	52	280	2833.70	1	2	.047	9
37	53	216	273.50	2	2	.044	9
102	53	281	699.80	1	2	.046	9
150	54	30	3289.20	1	1	.041	9
182	54	62	3465.40	2	1	.052	9
38	55	217	55.30	2	2	.042	9
103	55	282	714.60	1	2	.050	9
39	56	218	275.80	2	2	.041	9
104	56	283	1027.70	1	2	.045	9
151	57	31	3705.50	1	1	.045	9
183	57	63	8150.40	2	1	.042	9
40	58	219	330.20	2	2	.041	10
105	58	284	784.30	1	2	.046	10
41	59	220	281.50	2	2	.048	10
106	59	285	933.40	1	2	.047	10
152	60	32	1331.90	1	1	.042	10
184	60	64	1655.60	2	1	.035	10
42	61	221	395.60	2	2	.043	10
107	61	286	717.50	1	2	.048	10
43	62	222	316.10	2	2	.044	10
108	62	287	1043.40	1	2	.038	10
153	63	33	4401.30	1	1	.048	10
185	63	65	1295.60	2	1	.046	10
44	64	223	60.10	2	2	.053	11
109	64	288	892.60	1	2	.039	11
45	65	224	275.20	2	2	.044	11

110	65	289	1408.20	1	2	.037	11
154	66	34	4302.60	1	1	.049	11
186	66	66	2254.70	2	1	.034	11
46	67	225	49.90	2	2	.046	11
111	67	290	294.80	1	2	.041	11
47	68	226	305.40	2	2	.006	11
112	68	291	53.80	1	2	.043	11
155	69	35	1172.70	1	1	.039	11
187	69	67	3707.40	2	1	.039	11
48	70	227	223.30	2	2	.032	12
113	70	292	102.40	1	2	.044	12
49	71	228	209.90	2	2	.029	12
114	71	293	143.90	1	2	.049	12
156	72	36	3456.20	1	1	.052	12
188	72	68	931.70	2	1	.052	12
50	73	229	252.60	2	2	.043	12
115	73	294	1003.70	1	2	.042	12
51	74	230	263.00	2	2	.036	12
116	74	295	654.30	1	2	.041	12
157	75	37	4462.70	1	1	.043	12
189	75	69	1163.70	2	1	.049	12
52	76	231	54.40	2	2	.045	13
117	76	296	1884.20	1	2	.042	13
53	77	232	248.80	2	2	.040	13
118	77	297	719.60	1	2	.045	13
158	78	38	4940.40	1	1	.043	13
190	78	70	4679.00	2	1	.038	13
54	79	233	48.50	2	2	.052	13
119	79	298	208.30	1	2	.050	13
55	80	234	289.80	2	2	.020	13
120	80	299	95.40	1	2	.042	13
159	81	39	3511.60	1	1	.050	13
191	81	71	5191.70	2	1	.051	13
56	82	235	232.50	2	2	.050	14
121	82	1	277.70	1	2	.047	14
57	83	236	216.40	2	2	.041	14
122	83	2	217.50	1	2	.038	14
160	84	40	6348.10	1	1	.046	14
192	84	72	593.50	2	1	.044	14
58	85	237	233.30	2	2	.039	14
123	85	3	831.00	1	2	.052	14
59	86	238	244.10	2	2	.047	14
124	86	4	1644.00	1	2	.042	14
161	87	41	6701.30	1	1	.046	14
193	87	73	925.70	2	1	.056	14
60	88	239	32.20	2	2	.048	15
125	88	5	77.60	1	2	.044	15
61	89	240	275.30	2	2	.049	15
126	89	6	589.00	1	2	.040	15
162	90	42	1468.00	1	1	.049	15
194	90	74	276.60	2	1	.036	15
62	91	241	44.60	2	2	.043	15
127	91	7	106.60	1	2	.048	15
63	92	242	258.10	2	2	.035	15
128	92	8	683.30	1	2	.041	15
163	93	43	2485.60	1	1	.040	15
195	93	75	10379.40	2	1	.032	15
64	94	243	288.20	2	2	.040	16

129	94	9	1689.70	1	2	.045	16
65	95	244	361.20	2	2	.039	16
130	95	10	1139.10	1	2	.047	16
164	96	44	6159.50	1	1	.042	16
196	96	76	1236.20	2	1	.046	16
66	97	245	228.30	2	2	.003	16
131	97	11	40.80	1	2	.030	16
67	98	246	214.50	2	2	.035	16
132	98	12	931.30	1	2	.049	16
165	99	45	6337.30	1	1	.048	16
197	99	77	1115.50	2	1	.044	16

Weights

CASE_NO	PLANTID	POTNO	TREAT	FW	DW
1	1	100	1	.350	.060
68	1	100	1	.340	.090
2	2	100	1	.740	.120
69	2	100	1	1.260	.340
3	3	100	1	1.540	.210
70	3	100	1	12.560	2.100
133	1	56	2	.940	.130
166	1	56	2	1.140	.320
4	2	56	2	1.490	.260
71	2	56	2	2.010	.460
5	3	56	2	3.860	.680
72	3	56	2	21.850	3.720
134	1	58	1	1.650	.200
167	1	58	1	1.900	.500
6	2	58	1	.910	.130
73	2	58	1	1.680	.430
7	3	58	1	1.100	.140
74	3	58	1	4.860	.810
135	3	59	2	2.900	.470
168	3	59	2	26.590	4.790
8	1	59	2	.510	.080
75	1	59	2	.790	.180
9	2	59	2	.680	.150
76	2	59	2	1.560	.330
136	3	62	1	3.220	.430
169	3	62	1	22.570	3.680
10	1	62	1	.370	.080
77	1	62	1	.510	.130
11	2	62	1	.760	.140
78	2	62	1	1.060	.270
137	1	60	2	1.000	.160
170	1	60	2	.960	.220
12	2	60	2	.710	.110
79	2	60	2	.740	.180
13	3	60	2	1.840	.280
80	3	60	2	17.490	2.960
138	1	63	1	1.040	.170
171	1	63	1	.950	.190
14	2	63	1	.330	.070
81	2	63	1	.380	.070
15	3	63	1	2.110	.300

82	3	63	1	16.750	2.950
139	3	61	2	2.490	.390
172	3	61	2	24.570	4.280
16	1	61	2	1.440	.200
83	1	61	2	1.430	.300
17	2	61	2	.650	.090
84	2	61	2	.910	.170
18	1	64	1	.560	.100
85	1	64	1	1.420	.350
19	2	64	1	1.310	.200
86	2	64	1	1.820	.510
140	3	64	1	1.440	.240
173	3	64	1	16.510	2.500
20	3	65	2	1.940	.300
87	3	65	2	18.380	3.080
21	1	65	2	.180	.050
141	2	65	2	1.200	.190
174	2	65	2	3.300	.760
22	3	66	1	1.390	.180
88	3	66	1	11.650	1.870
23	1	66	1	.860	.160
89	1	66	1	2.070	.470
142	2	66	1	.710	.100
175	2	66	1	1.220	.570
24	1	67	2	1.370	.220
90	1	67	2	3.260	.720
25	2	67	2	.320	.050
91	2	67	2	.670	.170
143	3	67	2	.530	.080
176	3	67	2	4.210	.720
26	1	68	1	.530	.060
92	1	68	1	.900	.200
27	2	68	1	.890	.080
93	2	68	1	1.380	.280
144	3	68	1	3.430	.420
177	3	68	1	20.130	3.490
28	1	69	2	.260	.040
94	1	69	2	.220	.050
29	3	69	2	1.660	.230
95	3	69	2	15.000	2.630
145	2	69	2	.910	.130
178	2	69	2	2.150	.570
30	3	70	1	2.790	.400
96	3	70	1	1.130	.310
31	2	70	1	.330	.030
97	2	70	1	1.060	.240
146	1	70	1	.520	.080
179	1	70	1	2.170	.480
32	1	71	2	.	.130
147	1	71	2	1.990	.460
33	2	71	2	.	.060
98	2	71	2	.850	.200
148	3	71	2	.	.180
180	3	71	2	20.280	2.980
34	1	73	1	.	.090
99	1	73	1	1.790	.430
35	2	73	1	.	.100
100	2	73	1	1.270	.310

149	3	73	1	.	.240
181	3	73	1	13.770	2.460
36	3	78	2	.	.300
101	3	78	2	15.990	2.670
37	1	78	2	.	.170
102	1	78	2	2.160	.490
150	2	78	2	.	.110
182	2	78	2	1.490	.380
38	3	75	1	.	.360
103	3	75	1	21.510	3.560
39	2	75	1	.	.100
104	2	75	1	.940	.190
151	1	75	1	.	.120
183	1	75	1	1.830	.400
40	1	79	2	.	.110
105	1	79	2	1.350	.330
41	2	79	2	.	.140
106	2	79	2	1.280	.310
152	3	79	2	.	.340
184	3	79	2	20.050	3.460
42	1	76	1	.	.110
107	1	76	1	1.530	.330
43	2	76	1	.	.070
108	2	76	1	2.300	.520
153	3	76	1	.	.210
185	3	76	1	13.610	2.260
44	3	80	2	.	.170
109	3	80	2	15.500	2.410
45	2	80	2	.	.110
110	2	80	2	1.620	.370
154	1	80	2	.	.090
186	1	80	2	1.710	.360
46	3	77	1	.	.140
111	3	77	1	8.620	1.310
47	2	77	1	.	.000
112	2	77	1	.550	.100
155	1	77	1	.	.200
187	1	77	1	4.270	1.010
48	1	132	2	.	.100
113	1	132	2	1.390	.340
49	2	132	2	.	.090
114	2	132	2	1.060	.260
156	3	132	2	.	.390
188	3	132	2	16.070	3.070
50	1	131	1	.	.110
115	1	131	1	1.940	.420
51	2	131	1	.	.090
116	2	131	1	.820	.190
157	3	131	1	.	.440
189	3	131	1	18.820	3.360
52	3	134	2	.	.140
117	3	134	2	6.740	1.230
53	2	134	2	.	.220
118	2	134	2	2.220	.560
158	1	134	2	.	.160
190	1	134	2	2.130	.550
54	3	133	1	.	.340
119	3	133	1	15.830	3.030

55	1	133	1	.	.040
120	1	133	1	.470	.100
159	2	133	1	.	.170
191	2	133	1	2.870	.680
56	1	137	2	.	.150
121	1	137	2	.860	.180
57	2	137	2	.	.100
122	2	137	2	1.640	.340
160	3	137	2	.	.480
192	3	137	2	27.540	4.920
58	1	135	1	.	.100
123	1	135	1	1.250	.280
59	2	135	1	.	.110
124	2	135	1	2.330	.510
161	3	135	1	.	.440
193	3	135	1	20.400	3.560
60	3	130	2	.	.290
125	3	130	2	18.420	3.250
61	2	130	2	.	.090
126	2	130	2	.890	.200
162	1	130	2	.	.170
194	1	130	2	2.230	.480
62	3	129	1	.	.430
127	3	129	1	19.630	3.490
63	2	129	1	.	.060
128	2	129	1	1.100	.260
163	1	129	1	.	.150
195	1	129	1	1.750	.450
64	1	97	2	.	.090
129	1	97	2	1.550	.350
65	2	97	2	.	.130
130	2	97	2	1.790	.370
164	3	97	2	.	.310
196	3	97	2	16.800	2.870
66	1	98	1	.	.020
131	1	98	1	.270	.070
67	2	98	1	.	.140
132	2	98	1	2.370	.550
165	3	98	1	.	.530
197	3	98	1	26.360	5.010

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